MAY 3 1949

Vol. 76 MAY-JUNE, 1949 No. 3

Bulletin
of the
Torrey Botanical Club
and
Torreya

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Published for the Club bi-monthly
by
THE BUSINESS PRESS, INC.
N. QUEEN ST. AND McGOVERN AVE.
LANCASTER, PENNSYLVANIA

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The subscription price of the Bulletin of the Torrey Botanical Club (including Torreya) is $7.00 a year except to active members of the Club. Of the annual membership dues, $3.50 covers a year's subscription to the Bulletin.

Entered as second-class matter October 8, 1940 at the post office at Lancaster, Pa., under the Act of March 3, 1879. Accepted for mailing at the special rate of postage provided for in the Act of February 28, 1925, embodied in paragraph 4, section 538, P. L. & R.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 76, NO. 3, PP. 161–173 MAY 1949

RETICULOMYXA FILOSA GEN. ET SP. NOV., A NEW PRIMITIVE PLASMODIUM

RUTH N. NAUSS

In a field collection made in the metropolitan area of New York City during the summer of 1937, a remarkable versatile plasmodium was found. It has characters of both plants and animals, but no botanists or zoologists consulted, including the late Professor R. A. Harper, had seen any form resembling this extraordinary plasmodium. A report of its discovery has been withhheld (1) in the hope that its possible mode of reprotion other than by fission could be definitely determined, which has not yet been possible, and (2) that the literature could be searched more thoroughly, an opportunity for which was made available last year.

The new plasmodium appears to resemble very closely several species of Proteomyxa that were discovered in the latter half of the 19th century. The descriptions of these are often incomplete and even sometimes rather obscure. Because so little is seemingly known about such primitive organisms today, a somewhat detailed comparison of the early species with the new plasmodium will be made in a separate paper, the present one being confined to a description of the new organism and to a few characters it has in common with certain other forms, especially the Myxomycetes and the Foraminifera.

The discoverers of the proteomyxan species that closely resemble the new form gave each a different generic name, although it seems possible that some of them may belong to a single genus. Because of this and the incompleteness of some of the descriptions, owing to limited observation, I feel that it is necessary to regard the new plasmodium also as a new genus, for under varying circumstances and conditions it has revealed characters and habits apparently not recorded for the earlier forms. In recognition of one of its outstanding characters, namely the unusual abundance of the anastomosing, filose pseudopodia, I therefore propose for this new organism the name *Reticulomyxa filosa*, suggested by Dr. Libbie H. Hyman.

Reticulomyxa Nauss, gen. nov. Plasmodium nudum, multinucleatum, semper proteum, tunicam qualemcumque carens, ex areola centrali plasmatica continua compositum et reticulo peripherico, e pseudopodiis filiformibus anastomosantibus longissimis, unaique orientibus, complecto; plasmatis fluenta peripherica et centralia semper opposita; vacuola numerosa haud contractilia; plasma creberrime granulosa, nec in ecto- et endoplasma discrimen patiens.

[THE BULLETIN for March–April (76: 79–160) was issued March 10, 1949]

Naked, multinucleate plasmodium of everchanging shape. No wall or other permanently formed enveloping membrane. Central protoplasmic area surrounded by an intricate network of very long, active, anastomosing filose pseudopodia, which arise from any point on the surface. Pseudopodia possessing a simultaneous two-way or sleeve-type of flow: out through the center, back on the periphery. Many noncontractile vacuoles while vegetating, cytoplasm thickly granular, no differentiation into ecto- and endoplasm.

Reticulomyxa filosa Nauss, sp. nov. Plasmodium aquaticum vel semiaquaticum, album vel roseolum, in cultura semiaquatica in tumulos minutos contractum, aquatica in lamellam latam extensum, areola centrali ad 4 mm. (6 mm. maxime extensa) diam., fere immobili, canaliculis in quibus gluenta alterne opposita notata, pseudopodiis longitudinem decemplicem attingentibus, interdum crassitudines fusiformes areolasque alveolares exhibentibus, maturiora interdum cuncta migratoria, in plasmodia pauca (pro usu tria) fissa, vel in aquam novam translata in corpuscula sporoidea diffracta.

Plasmodium aquatic and semiaquatic, white, rarely shell pink. In semiaquatic cultures concentrated in small heaps, in aquatic often extended in a broad sheet, the central plasmodial area measuring to 4 mm. in diameter (6 mm. when fully extended), almost immobile, with many parallel channels in which the flows are alternately opposed; the pseudopodia attaining a length of ten times the central area, occasionally exhibiting fusiform thickenings and small alveolar areas; mature plasmodium homogeneously finely granular, periodically migrates to new site and divides longitudinally into daughter plasmodia (usually 3), disperses spore-like bodies when transferred to fresh dish of water.

Materials and Methods. The plasmodium of *R. filosa*, which has been in continuous cultivation since it was first found, was originally seen in a culture of slime-mold plasmodia which was started from decaying leaves on moist blotting paper. The leaves were collected in the woods in a depressed, soggy area, about five feet in diameter, that lies close to the edge of a tidal swamp. The ground is kept moist by a trickling stream from a spring, and old leaves and other vegetation fall here year after year. Since its discovery, *R. filosa* has been taken from this area several times along with slime-mold plasmodia, once even during a warm spell in January. It is not abundant nor is it found in every collection. This species was also obtained with slime molds about two miles distant from the spring, where its substratum was a damp, rotting ground log, since destroyed in drainage work. No sphagnum has been seen in or around these collecting areas.

R. filosa, together with its associated slime molds, was isolated by the same method as that used for *Hemitrichia vesparium* (Batsch) Macbr. and other species (Nauss 1943, 1947): moist, decaying vegetation was placed on white blotting paper in petri dishes, and kept supersaturated with tap water. Later it was found that it could be secured readily simply by

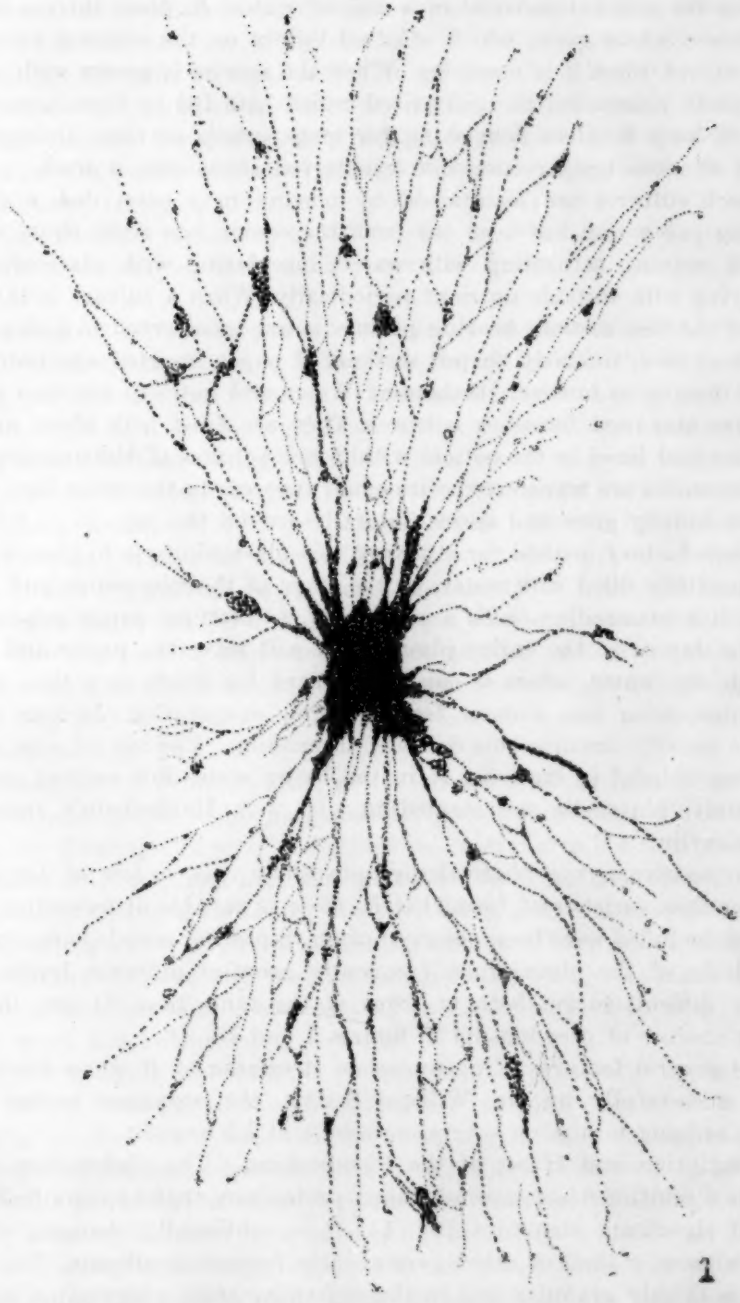


FIG. 1. Young, vegetating plasmodium, with anastomosing, filose pseudopodia; as seen in aquatic cultures. Granular masses of protoplasm scattered throughout pseudopodia. Approximately ×8.

placing the selected material in a dish of water. *R. filosa* thrives best on pulverized wheat germ, which is sifted lightly on the cultures every day or so except when it is maturing. When the species is grown with certain slime-mold plasmodia, the pulverized rolled oats fed to them seems sufficient to keep *R. filosa* flourishing for long periods of time. Cultures are grown at room temperature and transferred about once a week.

Stock cultures are maintained by placing in a petri dish a disc of blotting paper that has been cut from the center into eight equal wedge-shaped sections, saturating with water, inoculating with plasmodia, and supplying with suitable nutrient periodically. When a culture is thriving, four of the best sections bearing plasmodia are transferred to a clean dish with four new, similarly shaped sections of paper inserted alternately between them so as to cover the bottom. Water and nutrient are then added. Jars are also used for stock cultures. They are filled with about an inch of water and lined to the bottom with 2-inch squares of blotting paper. A few plasmodia are transferred with small tweezers to the water-line, where they eventually grow and spread laterally around the jar.

A satisfactory method for studying this plasmodium is to place a petri dish, partially filled with water, on the stage of the microscope and transfer to it a plasmodium with a portion of its blotting paper substratum. After a day or so the entire plasmodium will leave the paper and creep out into the water, where it can be observed for hours at a time with a water-immersion lens without fear of undue evaporation. Jarring of the culture usually disturbs this delicate plasmodium. The use of vital stains has been helpful in studying it in the living state. For critical cytological study, plasmodia are stained in situ with Heidenhain's iron-alum haematoxylin.

The accompanying photomicrographs show only a few of the seemingly endless varieties of form that *R. filosa* is capable of assuming. Most of those included have been observed often. Since the pseudopodia and the main body of the plasmodium frequently grow at different levels, it is usually difficult to get both in focus at the same time. Hence, the apparent absence of pseudopodia in figures 2 and 7.

The general features of protoplasmic streaming of *R. filosa* have been filmed successfully by Dr. William Seifriz, the organism having been made available to him on several occasions at his request.

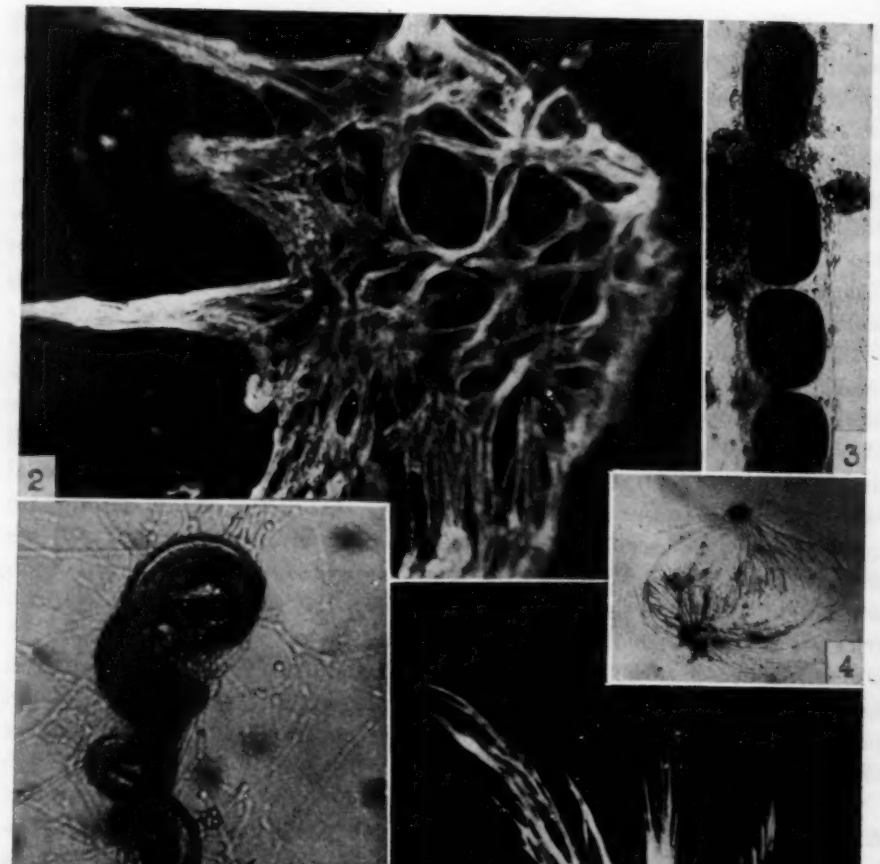
Description and Habit of the Plasmodium. The plasmodium of *R. filosa* is a multinucleate mass of naked protoplasm that appears to be devoid of significant structure (fig. 1). It is continually changing shape, being without a shell or other permanently formed membrane. The cytoplasm is thickly granular and in the vegetative stage contains an unusu-

ally large number of noncontractile vacuoles. Portions of protoplasm that become detached continue to develop. In all these respects *R. filosa* resembles the plasmodia of slime molds, except that the latter generally have fewer vacuoles. Unlike them, however, *R. filosa* has a central body portion that remains fairly stationary during vegetation, gathering its food by means of a highly organized system of anastomosing, filose pseudopodia that arise from any point on its surface and have a concurrent two-way flow. There is no apparent differentiation into ectoplasm and endoplasm, so that granules and vacuoles circulate freely out into the pseudopodia.

The central portion measures up to 4 mm. in diameter, but when extended, up to 6 mm. These measurements do not include the long, anastomosing pseudopodia that often extend to as much as ten times the diameter of the central area in search of food. Many of them may cross over and under others without fusing (fig. 13), or a group of them may parallel each other in their meanderings, gracefully taking the curves as one. En masse these can be seen with the unaided eye as a narrow band of delicate white strands perhaps an inch in length, suggesting a row of telegraph wires. Under the microscope they are observed to be connected by an intricate network of smaller and more delicate pseudopodial threads (fig. 9), which in turn may be connected by still smaller ones. Such parallelism has also occasionally been noted in shorter, exceedingly delicate pseudopodia that enclose areas where spore-like bodies appear to be in process of liberation (fig. 12).

In addition to being aquatic, as the similar proteomyxan forms were, *R. filosa* also grows semiaquatically. Its appearance often differs in the two types of culture. In aquatic cultures the central area is a thin, sometimes long sheet of protoplasm that adheres to the bottom of the dish, the anastomosing pseudopodia radiating laterally. When grown semiaquatically, on moist blotting paper, the central area forms into a heap which rises above the surface of the paper, the pseudopodia not being visible. As many as forty to fifty such plasmodial heaps, varying in size, may be seen in a thriving 3-inch petri dish culture.

In a vegetating plasmodium the pseudopodia generally appear somewhat lumpy from particles of food they are carrying (fig. 1). It is rather uncanny to observe the most delicate strands gyratingly cabling-in chunks of food that are sometimes as much as six times their own diameter. If the load is too heavy, as when worms and rotifers have been captured, the task of hauling is shared by a number of them. This is always an amazing and fascinating process to watch, for the pseudopodia are continually anastomosing and pulling apart from one another all the way along till it


2
3
4
(1cm.)
50μ
5
(1cm.)
200μ
6
(2.2 mm.)
1 mm.
7

would seem the captured prey might never reach its destination. Not infrequently food appears to be partially digested in situ before being transported.

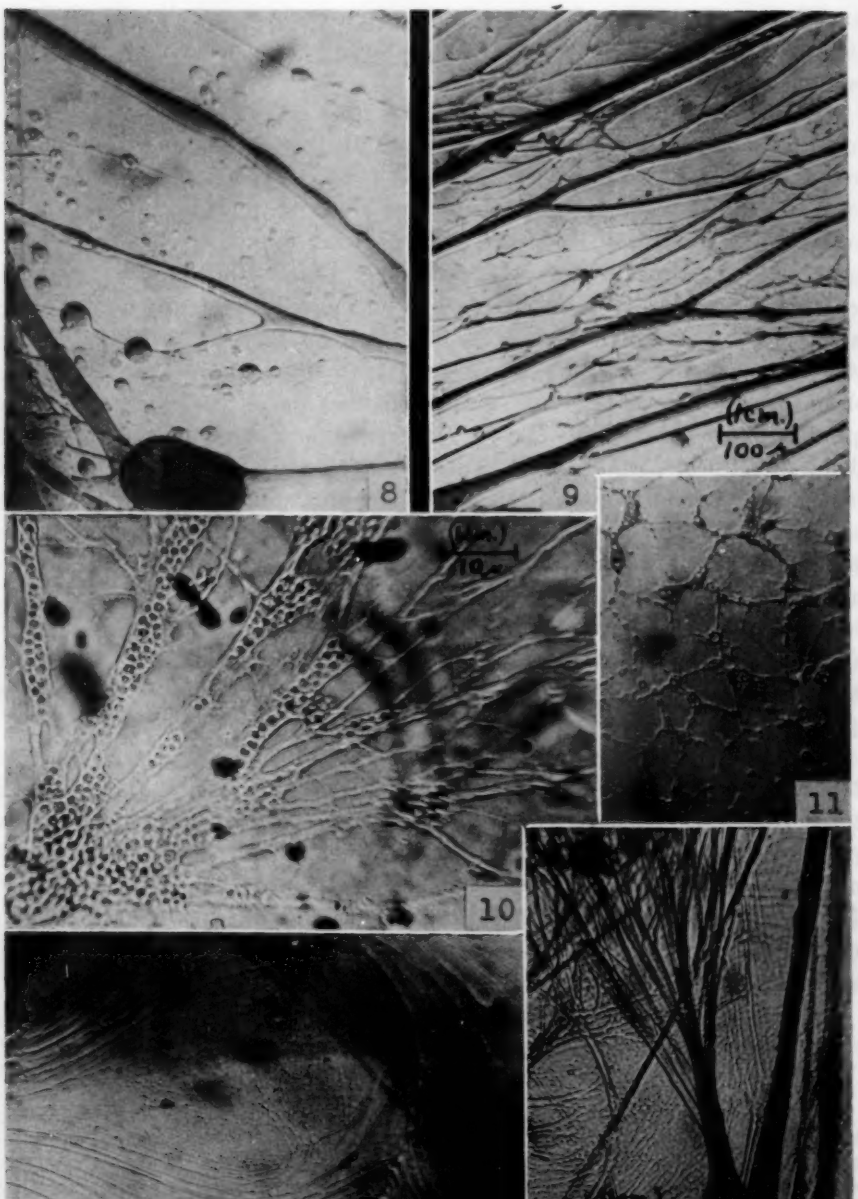
Some of the pseudopodia in fairly mature plasmodia do not seem to function as food-providers. These are usually larger and more in the nature of veins. At times a section of one will be composed of numerous fusiform or spindle-shaped bodies. In figure 8 the large diagonal vein (near top) gives some idea of their size and appearance, but they are frequently much more fusiform than these, with only a thin thread of protoplasm separating one from the other. A spindle may form at any point along large veins. As a rule, where one arises, others form in quick succession at the same point and then move on. Rhythmically the streaming protoplasm contracts at this point, each time pinching off and forming a new spindle. Thus a series of fusiform bodies comes into being. They glide along in tandem formation without incident until suddenly each in turn vanishes at a given point in the vein as rhythmically and as mysteriously as when first formed. These fusiform bodies are somewhat suggestive of those seen in species of *Labyrinthula* and *Chlamydomyxa* of the Proteomyxa, and also those observed occasionally in *Cribraria violacea* Rex of the Myxomycetes, a report on which is in preparation. In species of *Labyrinthula* and *Chlamydomyxa* they apparently glide along on filiform threads, often overtaking each other, whereas in *Cribraria violacea* they appear to remain stationary.

At times, instead of being fusiform or spindle-shaped, these bodies in *Reticulomyxa filosa* are globular and vary considerably in size for a given strand (fig. 8). Whether they represent a more advanced stage of the spindle form is not known. The globular forms appear to break down into smaller and smaller round ones that are finally abandoned by the thread of protoplasm that has carried them about (fig. 8, upper half). Their further development, which is very slow, has not yet been determined satisfactorily.

The plasmodium of *R. filosa* also has other significant features, one of which is the occasional alveolar character of the protoplasm. In figure 10

Explanation of figures 2–7

FIG. 2. Small plasmodium, as often seen on blotting paper cultures; anastomosing, filose pseudopodia not in focus. Approximately ×50. FIG. 3. Apparent encystment under water as a result of lowered temperature. ×200. FIG. 4. Young floating form, seemingly developed from spore-like bodies; two polar protoplasmic centers forming. Appoximately ×50. FIG. 5. Portion of a very small, mature floating plasmodium, with filose pseudopodia; stained with vital green. Approximately ×200. FIG. 6. Structure apparently composed of exceedingly fine filose pseudopodia, lying at edge of plasmodium and attached to it by strong protoplasmic "guy" lines (see also figure 13); stained with eosin. Approximately ×50. FIG. 7. Plasmodium dividing into three daughter plasmodia; long, anastomosing polar pseudopodia not in focus. ×22.


8
9
(1cm.)
100
10
(1cm.)
10
11
12
(1cm.)
200
13

protoplasm so characterized is seen emerging from the plasmodium and fanning out into the pseudopodia. Small sections of it then girate back and forth along the strands, finally being abandoned by the filose threads (fig. 11, lower right).

Another interesting form is that shown in figure 6, seemingly made up of exceedingly fine pseudopodia. These structures, which are observed only now and then, are somewhat variable in size and shape, and lie adjoining the plasmodium, as in figure 6, or at a short distance from it. In either case they retain a connection with the mother plasmodium. They later appear to form short, delicate nonanastomosing filopodia that wave freely about in the water, seeming to give off minute spore-like bodies similar to those in figure 12 mentioned earlier, which are too small to be seen clearly in the illustration. They also resemble those that appear when a mature plasmodium ruptures, described in the following paragraph. Further development of these spore-like bodies has been difficult to follow.

A mature plasmodium is waxy white in blotting paper cultures, its protoplasm being thick and opaque (fig. 5) and homogeneously finely granular. When such a specimen is transferred to a fresh dish of water, it bursts, dispersing minute spore-like bodies over the surface of the water and scattering large fragments of residual protoplasm that proceed to round up again and send out a few filose pseudopodia. After several days, young floating plasmodia are found (fig. 4), which are different in character from the residual protoplasm. Myers (1938) gives a somewhat similar picture of a marine species of Foraminifera, *Tretomphalus bulloides*, which has a test or shell. He states that when the asexual stage reaches maturity *T. bulloides* rises to the surface, where thousands of gametes are given off and that residual protoplasm continues to give rise to filose pseudopodia. Myers also says that although he has studied this species over a period of five years he has not been able to demonstrate development of the gametes beyond their union in fertilization. It is interesting to note that *Reticulomyxa filosa* further resembles the Foraminifera in possessing the same type of flow in the pseudopodia, the occasional pinkish tinge of the protoplasm, and in being multinucleate.

Explanation of figures 8–13

FIGS. 8–13. A few of the varied patterns of pseudopodia and veins. FIG. 8. Globular and somewhat spindle-shaped bodies; small round ones (upper half) abandoned by protoplasmic threads. Approximately ×200. FIG. 9. Parallel pseudopodia connected by finer protoplasmic meshwork. Approximately ×100. FIG. 10. "Fan" pattern of alveolar protoplasm; stained with vital green. Approximately ×1000. FIG. 11. "Triangle" patterns of alveolar protoplasm in pseudopodia; eosin stained. Approximately ×200. FIG. 12. Curved pattern of parallel, filose pseudopodia enclosing meshwork of delicate anastomosing pseudopodia which appear to be liberating minute spore-like bodies too small to be clearly seen here. Approximately ×50. FIG. 13. Enlarged area of protoplasmic guy lines of figure 6; eosin stained. Approximately ×200.

The pseudopodial streaming in *R. filosa* is a simultaneous two-way or sleeve-type of flow: concurrently moving outward through the center and back on its wall or periphery, the protoplasm being more or less equally divided between the two streams. This type of flow, which is also common to a number of other organisms, is apparently present in the pseudopodia of *R. filosa* at all times. It is not so easily detected, however, in large veins of protoplasm that periodically carry the plasmodium to a new location, the process of which will be described later. At such times, the protoplasm seemingly appears to flow in one direction only, outward, with no return or peripheral flow taking place. Under very high magnification, though, even here the return flow has sometimes been observed, being scarcely more than a very thin film. In character this would seem to indicate that the strong urge to move outward is capable of almost obliterating the return flow, and possibly at times it virtually does.

Such is the picture of streaming in pseudopodia. That observed in the main or central part of a vegetating plasmodium is somewhat different. Here is a broad, thin sheet of protoplasm, consisting of many parallel channels of flow alternately opposed. As many as twelve have been counted in one very broad sheet. Streaming is continuous and rapid. The protoplasmic granules of one channel race very close by those of another. As no visible wall separates them, the result is nothing short of spectacular. Such wide bands of protoplasm with alternately opposed flow do not seem to have been described for similar organisms.

Movement never ceases. As the streaming protoplasm reaches the periphery of the central area, it often turns and finds its way back through some other channel. I have several times noted a somewhat comparable circulatory movement in the slime mold *Dictydium cancellatum* Macbr., which has been collected close to the spring where *R. filosa* was discovered. In small areas of this purple pigmented plasmodium the veins are divided longitudinally into two channels, the protoplasm in each flowing continuously in opposite directions, with no reversal of flow taking place. As in *R. filosa*, the protoplasmic granules of the two opposing currents move along quite closely to each other with no visible membrane separating them. Outside of such areas, however, the veins have only one channel of flow, the streaming manifesting the characteristic tidal flow of slime molds. I have not observed this unusual type of flow in any other species of Myxomycete thus far cultured, nor have I seen it reported in the literature.

The plasmodium of *R. filosa* has one outstanding habit, previously alluded to, namely, that of periodically moving off to a new location. Preparatory to this change of position, the filose pseudopodia are nearly

all withdrawn and the plasmodium appears to rid itself of all extraneous matter. This cleansing process is carried on by a kind of self-filtering or screening as the plasmodium begins to move forward to the new site. The result is a homogeneous, finely granular plasmodium and a discarded pattern or false body that is an exact replica of the departing plasmodium. This replica, being made up of excreted materials, is comparable in a way to the residue left as tracks by a slime mold, except that it is more in the nature of a cast of the entire departed plasmodial body than of the network of veins.

To transport itself to the new location, which may be as much as one inch away, the cleansed protoplasm of *R. filosa* flows through several large veins, which seemingly appear to move outward only. A short time after it begins to arrive at its destination it prepares for longitudinal division, which usually results in three daughter plasmodia of about equal size (fig. 7). This process of division, requiring from 8–12 hours to complete, begins anteriorally, the two outer daughters drawing away from the middle one at a slight tangent (fig. 7), so that by the time the last of the small connecting strands are severed, each daughter plasmodium is moving off in a divergent direction. Each creeps slowly about for a few days and then settles down to a more or less stationary existence, leaving to the energetic filose pseudopodia the task of finding and bringing in food. This habit of moving off and dividing does not seem to have been described for similar proteomyxan organisms.

Daughter plasmodia that have only recently become separated are elongated in shape and their filose pseudopodia are concentrated mainly at the anterior and posterior ends. These pseudopodia can scarcely be seen in figure 7 because they are growing at a different level from that of the plasmodial body. After several days, when a daughter plasmodium has settled down, it gradually becomes less extended and the pseudopodial threads begin to branch out gradually from other parts (figs. 1, 2), eventually forming the immense surrounding network that is so characteristic of this organism.

R. filosa seemingly does not withstand slow desiccation as most slime molds do. I have isolated two species of slime molds, however, that react as *R. filosa* does; they apparently cannot form viable sclerotium when slowly dried. These are the brown pigmented plasmodium of *Didymium nigripes* Fr., which is regularly found around the spring where *R. filosa* occurs, and an unidentified white plasmodium (Lab. No. 84), which was collected about fifty feet from this spring in 1939. Neither of these species seems to survive when dried after the manner of other Myxomycetes. They are therefore kept in the plasmodial stage only. *Didymium nigripes*

generally gives rise to sporangia within a few months after having been collected, while No. 84, which has been found only once, has never fruited in the laboratory. Unlike any other slime mold I have cultured, No. 84 thrives only when supplied with wheat germ, the optimum food of *R. filosa*. Whereas *R. filosa* requires food several times a week, however, No. 84 can be kept from 4–6 months on a single feeding.

On several occasions the new plasmodium has apparently encysted under water, as do some slime molds. Once during the winter when a culture of it was set on an inside window sill for a few days, the plasmodium broke up in situ along the veins (fig. 3) similarly to the unusual slime mold *Hemitrichia vesparium* (Nauss 1943). Also, when cultured several times along with algae, it has rounded up into small, irregularly shaped masses. Although both types of apparent encystment, on being restored to normal cultural conditions after a few weeks, developed into healthy plasmodia, such dormant bodies do not seem sufficiently dependable for maintaining the species in the laboratory.

It has been stated several times in this paper that *R. filosa* seemingly gives off minute spore-like bodies whose development has been difficult to follow. There also appears to be evidence in my cultures that slime molds may manifest a somewhat similar phenomenon. Such a phase in the Myxomycetes could, it seems, explain why some of them appear to lose vigor at certain times, either in whole or in part, and tend to die out if not given the care they need at this time. A full elucidation of this problem awaits further observation and experimental study.

R. filosa has been shown to have several characters in common with the Myxomycetes and Foraminifera. It is likely that more will be found. It seems possible that further studies may also reveal that this primitive organism, together with certain species of Proteomyxa which it resembles rather closely, may in time come to be regarded as members of a group that is more or less intermediate between the Myxomycetes and the Foraminifera.

SUMMARY

A hitherto unreported primitive plasmodium, *Reticulomyxa filosa,* has been discovered, which has among others the following characteristics and habits:

1. Aquatic and semiaquatic (fresh water), multiform, white plasmodium, without wall or other permanently formed membrane, remaining fairly stationary while vegetating, surrounded by an intricate network of anastomosing, filose pseudopodia arising from any point on the surface of plasmodium and extending to as much as ten times its diameter in search of food.

2. Protoplasm very active, finely and coarsely granular, undifferentiated into ecto- and endoplasm, multinucleate, vacuoles (noncontractile), not surviving slow desiccation.

3. Streaming in pseudopodia a simultaneous two-way or sleeve-type of flow; in central portion, which is often a thin broad sheet of protoplasm, many lines of flow alternately opposed and irreversible.

4. Plasmodium periodically clears itself of extraneous matter, moves to a new site, and undergoes longitudinal fission, usually resulting in three daughter plasmodia. Mature plasmodia seemingly disperse spore-like bodies when transferred to a fresh container of water, but the nature of reproduction other than by fission only vaguely understood at present.

5. Under water, plasmodial activities arrested both when subjected to lowered temperature and when cultured with certain algae.

6. Similarities to species of Myxomycetes and Foraminifera pointed out. Close affinity with certain species of Proteomyxa strongly suspected.

Acknowledgments. I wish to express my thanks and appreciation to those listed below, whose combined aid and encouragement have helped materially in making this report possible: Dr. John S. Karling, then of Columbia University; Dr. D. H. Wenrich, University of Pennsylvania; Dr. G. W. Martin, State University of Iowa; Dr. Joseph A. Cushman, Cushman Laboratory for Foraminiferal Research; Dr. William H. Weston, Harvard University; Dr. John Tyler Bonner, Princeton University; Dr. William D. Burbanck, Drury College; Dr. Asa A. Schaeffer, Temple University; Dr. Mary A. Pocock, R. U. C., Grahamstown, South Africa; Dr. Robert Chambers, Woods Hole; Dr. Libbie H. Hyman, American Museum of Natural History.

I am also gratefully indebted to Dr. William Seifriz, University of Pennsylvania, for his aid in the earlier preparation of this report. To Dr. Donald P. Rogers, New York Botanical Garden, I owe special thanks for the help he has given in numerous ways, particularly for assisting in the translation of the early literature and for preparing the Latin diagnoses.

THE NEW YORK BOTANICAL GARDEN
NEW YORK CITY

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BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 76, NO. 3, PP. 174–176 MAY 1949

DETECTION AND OCCURRENCE OF ACID-PRODUCING FUNGI[1]

J. W. FOSTER AND HENRY DAVIS

For certain physiological problems and for surveys seeking organisms of potential industrial application it is desirable to examine large numbers of new strains of organic-acid-producing fungi. Three objectives may be satisfied by such a survey: (1) higher-yielding strains may be obtained with respect to any particular acid; (2) organisms may be obtained different from any known to produce a certain acid; (3) new acids may be found to be produced by fungi.

The following selective technique for isolation of acid-producing fungi has proved very satisfactory. It is based on color change of brom cresol green in the pH range between 5.4 and 3.8. Formation of organic acidity in a medium initially adjusted to pH 4–5 causes a marked change from blue-green or green to bright yellow. In agar plates the contrast is striking and the test very sensitive. Non-acid-formers cause no yellowing and simple inspection at once differentiates acid-forming fungi from non-acid-formers.

Since natural materials such as soil, manure, air, etc. are used as source materials, it is necessary to eliminate the bacteria and actinomycetes. This is accomplished by the original Waksman technique of adjusting the agar after sterilization to pH 4.0–4.5 with 1N HCl. The following points relate to the best working conditions. Medium: 5% glucose, 0.5% peptone, 0.1% KH_2PO_4, 0.05% $MgSO_4 \cdot 7H_2O$, 2% agar. The organic nitrogen source favors rapid growth and recovers maximum numbers of fungi. The high glucose concentration forces maximum acid formation by the fungi under these conditions.[2] The indicator is rather concentrated. One gram brom cresol green is ground in a mortar with 14.3 ml. 0.1 N NaOH. When solution is complete, it is diluted to 250 ml. with distilled water. The optimum concentration was found to be 6.7 ml. of this stock indicator solution per 100 ml. agar medium, added before autoclaving. This concentration had no detectable inhibition on the fungus population nor was it absorbed out of solution by the fungus mycelium like many of the other ordinary pH indicators tested. Pour plates of various dilutions of natural materials are prepared in the usual manner and incubated at 30° C.

Acid-producing colonies are detectable while they are still barely visible

[1] Supported in part by a grant from Ciba Pharmaceutical Laboratories, Inc., Summit, N. J.

[2] Foster, J. W. 1947. Some introspections on mold metabolism. Bact. Rev. 11: 167–88.

to the naked eye; for this reason early observation is desirable. This permits testing in relatively crowded plates where largest numbers of fungi are exposed for examination, the results being obtainable before overgrowth occurs. Use of 150 mm. petri dishes permits detection of acid-formers even though numerically they may be only a small proportion of the total fungus population. The matter of time-saving on incubation is an important feature.

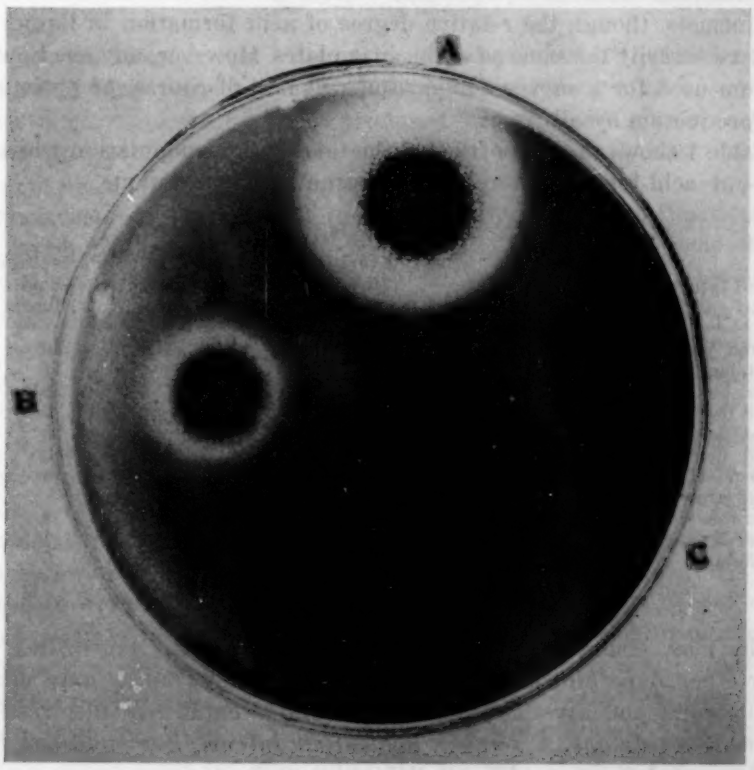

FIG. 1. Yellow zones indicative of acid production by fungi. The background agar is deep blue-green, somewhat darker on the right side owing to uneven distribution of agar thickness. A, strong acid-producer with largest zone. B, moderate acid-producer. C, non-acid-producer.

Generally the picture of the young colony is characteristic of the old one, though weak acid-formers may not be detectable as very young colonies. Nevertheless, the desired organisms, namely strong acid-producers, are unmistakably detected while colonies still one millimeter or less in diameter. The yellow acid zone surrounding the colony increases with the size of the colony; it is proportional in size and in intensity to the acid-forming ability of the organism (fig. 1).

The acid-formers are picked off before colonies grow together and inoculated on to petri plates of the same medium but adjusted to pH 6.5 at which value the indicator is its full deep blue; restriction of bacteria is unnecessary here. The acid-formation reaction in these plates is even more sensitive because the zones around larger colonies give a more reliable evaluation of the organisms than on the original crowded isolation plates.

Numerous checks in liquid media confirm the fact that the method selects acid-formers, though the relative degree of acid formation in liquid media is not necessarily the same as in the agar plates. However, any one liquid test medium used for a survey comparison will not, of course, be optimum for acid-production by all fungi.

Table 1 shows the proportion of the total fungus population which were clear-cut acid-formers as revealed by the above technique.

TABLE 1. *Acid-forming fungi in soils.*

Soil type	Optimum dilution	Average total count	Numbers of acid producers	Percentage of acid-producers
Manured garden	1/1000	25	4	16
Florist leaf mold	1/10000	18	2	11
Flower bed	1/1000	40	11	28
Flower bed	1/1000	17	1	6
Plowed field	1/1000	9	3	33
Plowed field	1/1000	15	2	13
Cotton field	1/1000	14	2	14
Wooded area	1/10000	14	1	7
Rut on roadside	1/1000	11	1	9
Bank of stream	1/10000	20	1	5
Corn field	1/1000	17	1	6
			Average:	13.4

The most common acid-producer encountered was *Aspergillus niger*. Many other *Aspergilli* and *Penicillia* were in this group as were members of Mucorales and several unidentified fungi. Tentatively identified were *Aspergillus hidulans, A. terreus, Penicillium luteum, P. rugulosum, P. frequentens,* and the yeast-like *Pullularia pullulans.*

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BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 76, NO. 3, PP. 177–195 MAY 1949

THE TRICHOMES OF PHYSARIA GEYERI, PHYSARIA AUSTRALIS AND LESQUERELLA SHERWOODII: DEVELOPMENT AND MORPHOLOGY

SOPHIE JAKOWSKA[1]

Trichomes or epidermal hairs on the aerial parts of plants attracted the attention of early writers because of the peculiar structure and the characteristic silvery appearance they produced in pubescent plants. Thus the general morphology of trichomes was treated in the early descriptions of the plant epidermis from 1700 onward.

Since then, and particularly in the last century, various functions have been attributed to the trichomes. It is of interest to review some of these older opinions, although even today we do not possess sufficient evidence to establish any theory of the functions of trichomes. Poisson (1879) believed that hairs on plants such as *Phaseolus* were an adaptation to the environmenal conditions. Arthur (1881) suggested that upon rapidly growing parts of plants, such as young flower buds, the abundance of delicate trichomes aids in supplying oxygen to the tissues. He believed this was analogous to oxygenation of some polyps and worms having external filamentous gills. Berthold (1882) on the other hand believed that trichomes protect the plant from excessive light. Tietze (1906) brought forward some evidence that trichomes were concerned with water intake in Bromeliaceae. Cannon (1908) referred to trichomes as a trichomal system. He believed that the trichomal system offers a favorable field in which to study the origin, development and biological relationships of plant organs, inasmuch as it is comparatively little affected by other tissue systems. He pointed to the fact that in some species trichomes take on the function of photosynthesis, thus becoming entirely independent for their nutrition. Harvey (1919) performed experiments from which he concluded that undercooling of the tissues occurs to a greater degree in herbaceous plants with trichomes. Sayre (1920) believed that trichomes are related to transpiration of the leaves.

Most of the older workers who considered trichomes as a means for classification have availed themselves of both herbarium specimens, including sections prepared from such dried specimens, and fresh living material. More recently Molby (1931), who studied trichomes in Malvaceae, boiled

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[1] The author is indebted to Dr. Bassett Maguire, who supplied the material for this study. Thanks are expressed to Drs. C. A. Berger S.J. and J. J. Biesele for suggestions concerning the manuscript.

fresh leaves for a few minutes in water, then removed the trichomes under the binocular. The trichomes were placed in a small drop of water on a slide and allowed to dry, then mounted in Canada balsam. Wright (1945) studying the epidermal characters in *Fraxinus* followed a method which consists in obtaining collodion peels made by applying a solution of collodion in butyl acetate plus 5 per cent butyl alcohol to the under surface of the leaf.

In the present study living and herbarium specimens have been used, but greatest emphasis has been placed on the cytological preparations consisting of leaf sections and smears, which permitted observation of changes within the nucleus at various stages of trichome development.

Most previous investigators were concerned for taxonomical reasons with the morphology of fully differentiated trichomes, rather than with their origin and development. Very few were concerned with the nuclear phenomena.

Arthur (1881) described incipient trichomes on the surface of anthers, which arose through an enlargement of some epidermal cells protruding to the outside. Tietze (1906) described the development of a multicellular stellate trichome in Bromeliaceae, which arises from epidermal cells. Cannon (1908) attempted to determine the sequence of the cell wall formation in a multicellular trichome in walnuts and sketched 6- and 8-celled trichomes showing the cell lineage of each. Rosenvinge (1911) studied hyaline unicellular simple hairs in a family of marine algae. He noticed that they arose through the metamorphosis of superficial cells and were not cut off from the apical cells as special hair cells. In the fully grown trichomes he observed only a thin layer of protoplasm and limpid cell sap within the cell, but during the process of development he observed changes in the position and in the shape of the nucleus, which according to him becomes transformed into a crystalloid in the latest stage and then stains deep blue with hematoxylin. He also noticed that these hairs often decay long before the cessation of growth. Brockmann-Jerosch (1914) affirmed that in the grasses he studied trichomes arise on the young leaf blade from a young cuboidal epidermal cell through a protrusion of the outer wall. He described the changes in the walls of the trichomes without considering the nuclei. In some of the grasses described by him the unicellular simple trichomes attain extremely large size.

A fairly recent paper in which the development of the trichomes was described in detail and from a cytological viewpoint was that of Cooper (1932) on *Shepherdia canadensis*. This author followed the stages of development of a multicellular peltate trichome, giving great attention to the relative position of the nuclei and the orientation of the spindles during divisions. He traced the cell lineage and determined the origin of the cells of the stalk and of the shield in the formed peltate trichome.

Trichomes in *Physaria Geyeri, P. australis,* and *Lesquerella Sherwoodii* are unicellular stellate structures. Beginning as epidermal cells the trichomes in these species reach an unusual size and exhibit during the whole process of growth and differentiation nuclear changes of considerable cytological interest.

The characteristics of the trichomes permit differentiation between the three species under investigation. For the same reason Vanatta (1907) and Payson (1921) attached great importance to the trichome size and shape as a means of differentiating species within the genus *Lesquerella.* Although it has been impossible in the present study to establish one single trichome type for each of the three species, there is no doubt that the general characteristics of the pubescence may play an important part in the taxonomical determinations.

Rollins (1939) states that *Physaria* and *Lesquerella* are not easily recognized as distinct genera if only flowering plants are considered, though their fruits differ. But even in these respects certain species of *Lesquerella,* namely *L. Kingii* and its close relatives, approach the condition found in such species of *Physaria* as *P. Geyeri.* This relationship was pointed out by Payson (1921). As Rollins states on the basis of his cytological studies of meiotic chromosomes, the cytological evidence also indicates a closer relationship between the two genera than that attributed to them by some taxonomists, although there is no question as to the separation of these two genera.

With these facts in mind it has been attempted in the present study to bring in a few similarities and differences in trichome form and development in the representatives of the two genera in question. The main purpose of this investigation was, however, to follow the nuclear phenomena in the unicellular stellate trichomes of *P. Geyeri, P. australis* and *L. Sherwoodii* through the process of growth and differentiation.

Material and Methods. Living and herbarium specimens of *P. Geyeri, P. australis* and *L. Sherwoodii* were made available through the courtesy of Dr. Bassett Maguire, Curator of the New York Botanical Garden, who collected and identified the plants. The living specimens were raised to maturity from seeds in the greenhouses of the New York Botanical Garden.

The places of origin of the plants were as follows: *P. Geyeri, 26715,* Nine Mile Falls along the Spokane River, Washington, July 22, 1946; *P. australis, 25408,* O'Donall Canyon, West Slopes, Paradise Range, Nevada, June 12, 1945; *L. Sherwoodii, 27057,* above Slick Rock Creek in vicinity of Hurricane Creek, Wallowa Mountains, Oregon, August 16, 1946. The parent plants from which the seeds were derived were available also as herbarium specimens, except for *P. australis.*

The cytological studies on trichomes were done by means of Feulgen smears after 3 : 1 alcohol-acetic fixation. Light green counterstain was used to show the cytoplasm to a greater advantage. Smears were made of various portions of the 6-week-old plants and of the leaves from the older plants. Sections of the young plants were made and stained with iodine and gentian violet.

The observations, measurements, and counts were carried out under 15x ocular and 98x objective for cytological material and with a 15x ocular and 10x objective for the herbarium and living material.

Observations and Results. In the course of the investigation it became necessary to compare the general morphology of the trichomes fixed in acetic alcohol, and stained by the Feulgen reaction, with the living and dried specimens. Trichomes have not been studied previously by the smear method and it was necessary to determine to what extent the trichome shape was altered in the smear preparations. At the same time a more careful study of living and herbarium specimens has been encouraged by the evident need of more information on the morphological features of the two genera *Physaria* and *Lesquerella* and the fact that some authors greatly relied on the trichome shape and size for the differentiation of the species within these genera. Since the comparison between the smeared, living, and the herbarium material seemed to indicate that it is possible to obtain good cytological preparations without significant alteration of the shape of the trichomes, it has been judged proper to describe the various stages of trichome development as they appeared in the Feulgen-stained smear preparations.

Cytological Observations on the Development of the Trichomes. In the 6-week-old plants, most of which were less than 1 inch above the soil and still bearing the cotyledons, it was already possible to observe all stages of development of the epidermal hairs on the stem and leaves. *Physaria Geyeri* is the species for which the whole process is described in detail. In the two other species of plants under investigation the process was essentially the same. The trichomes of *P. Geyeri*, however, were the simplest of the three and this facilitated the description.

The trichomes originate from the epidermal layer of the actively growing regions of young leaves and stem. They do not occur on cotyledons, as was already pointed out by Rollins (1939) for plants of the same genera. The trichomes do not develop synchronously, for the various stages of development can be found together. An actively growing region of the leaf bud in a 6-week-old plant is reproduced in figure 1. It can be seen that some of the epidermal cells elongate in the direction of the free leaf surface. The main portion of the cell remains in its position among the epidermal cells and

forms the stalk of the future structure. The nucleus at the early stage is located within the portion of the cell adjacent to the epidermal cells. Later, the cell elongates and sends out projecting arms parallel to the leaf surface.

In the section seen in figure 1 only two of the developing parallel branches or arms can be observed. These continue to grow parallel to the surface of the epidermis and apparently remain straight, giving the effect of a star-shaped shield. Even at the stage seen in figure 1 the section of the trichomes shows only a bulb-like enlargement, partially expanded. The structure of the developing shield is rosette-like, when viewed from the top,

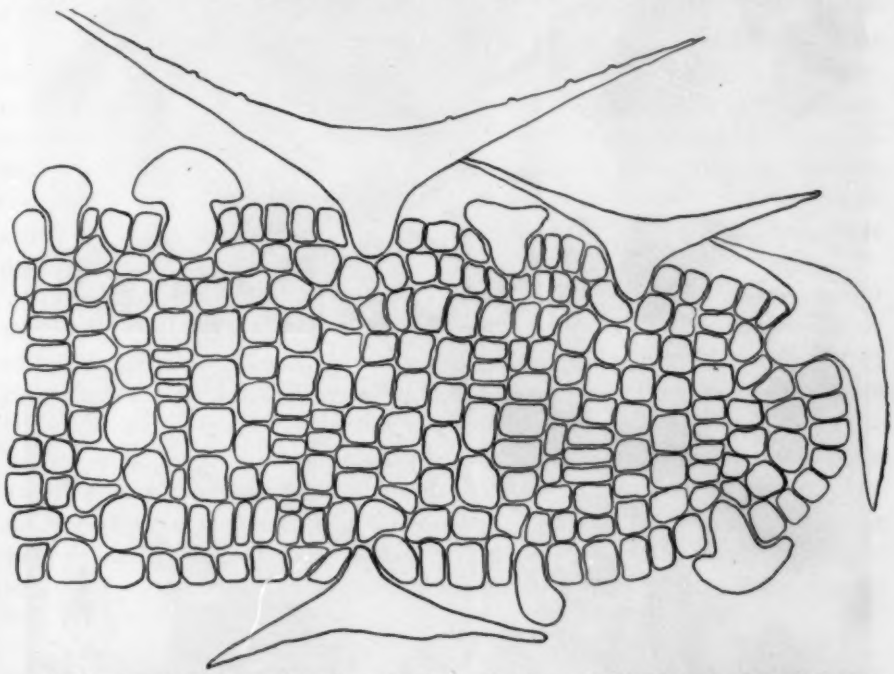
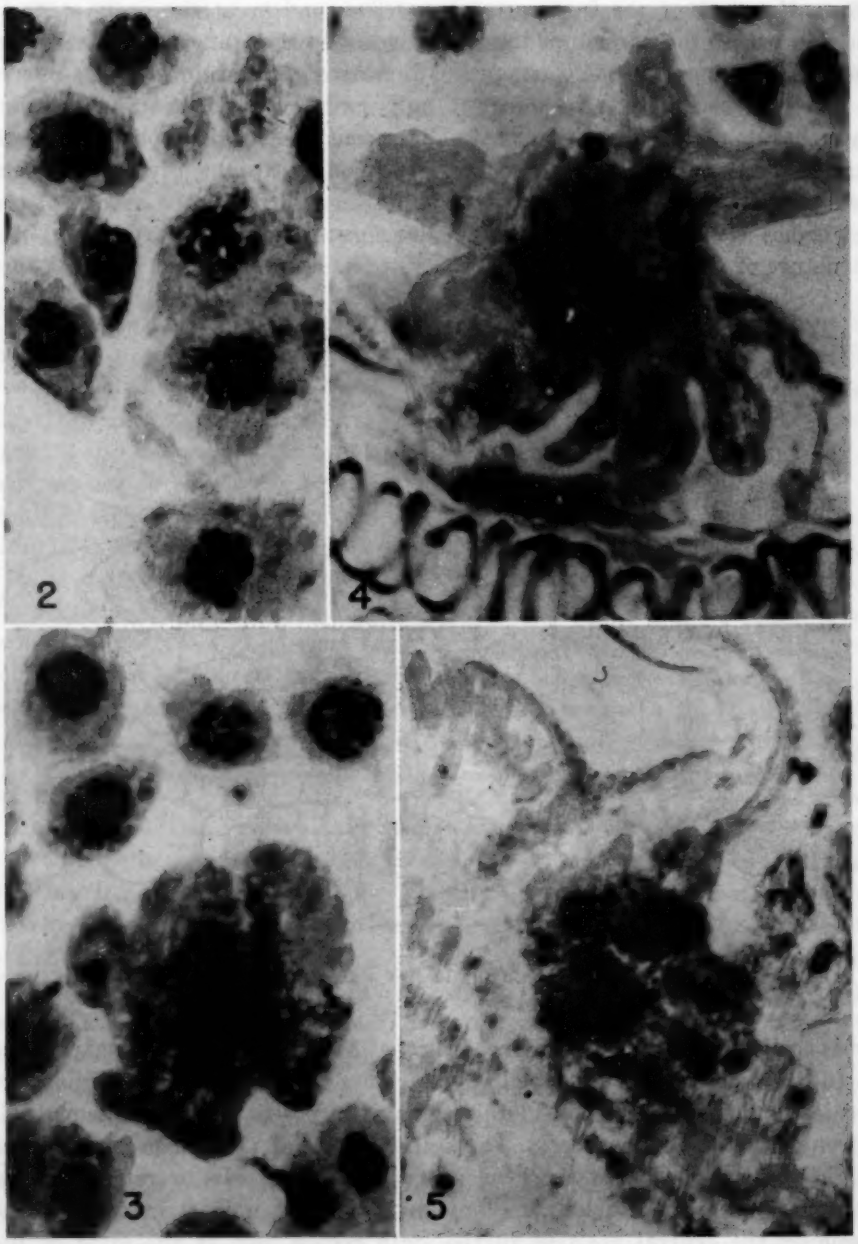


FIG. 1. Longitudinal section through a leaf of a six-week-old *Physaria Geyeri*. Camera lucida drawing. × 750.

as is easily seen in the smear preparations. At the stage when the trichome is fully developed the outer cell wall becomes thickened, forming knob-like projections. There is no considerable change in position of the trichome cell throughout the entire process. The stalk portion of the cell becomes either slightly depressed below the level of the epidermal cells or retracted to a certain extent. The nucleus, as long as it remains normal in appearance, occupies the central position in the stalk region, but at the level of the developing trichome branches. No septa are formed within this large unicellular structure. The relative increase in size of the trichome cell from the



FIGS. 2–5. Leaf smears from adult specimens of *Physaria Geyeri* stained by Feulgen reaction and light green. All × 1960. FIG. 2. Epidermal cells showing heterochromatic bodies. FIG. 3. Expanding epidermal cell. FIG. 4. Cell showing development of trichome branches. FIG. 5. Condition of the nucleus of a developing trichome at a later stage: enlarged heterochromatic bodies and nucleolus.

initial to the final stages of the development, and the cytological phenomena involved, are best followed in the smear preparations which allow a surface view of the trichome's branching portion.

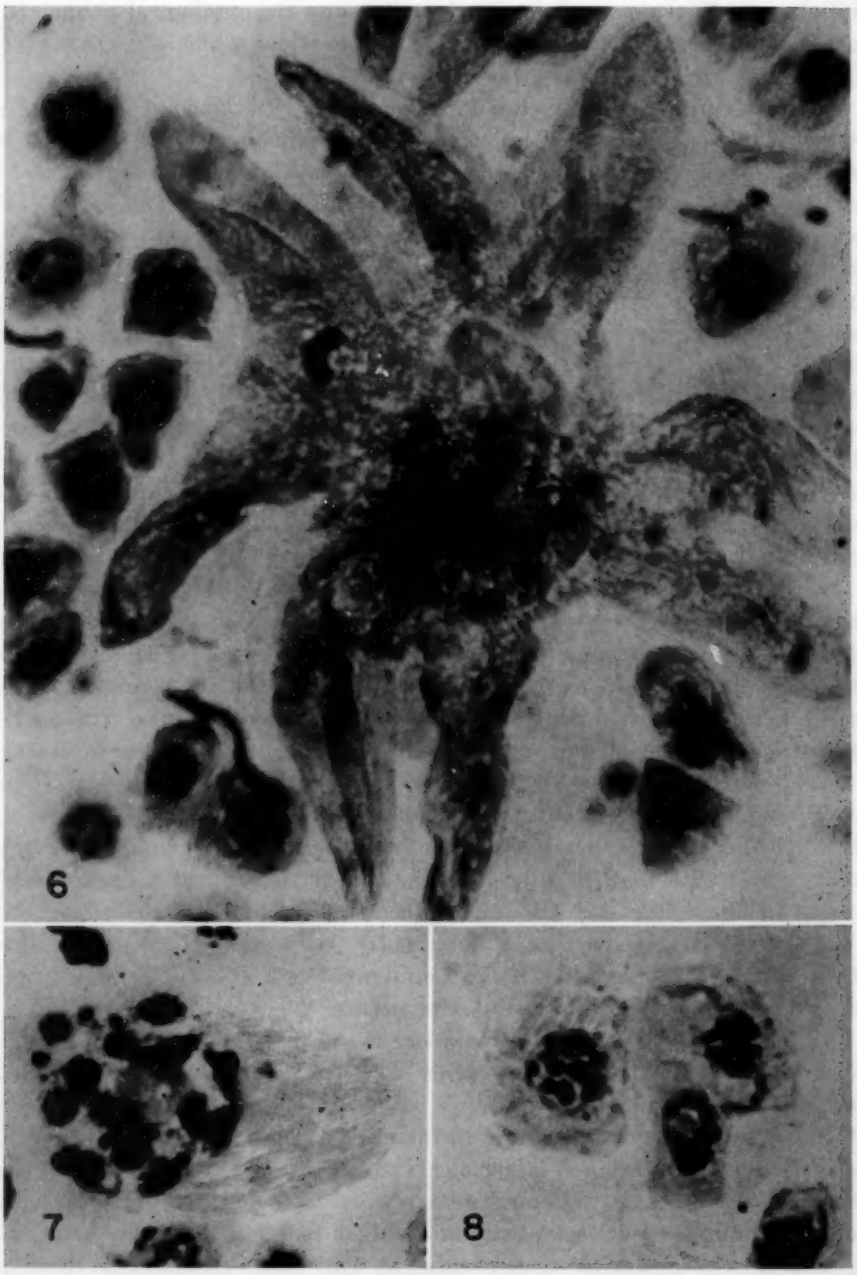
The consecutive stages in the development of a trichome of *P. Geyeri* as observed in Feulgen-stained leaf smears are shown in figure 2–6. It can be seen in figure 2 that the nuclei of the epidermal cells are in a characteristic prochromosome stage. The nucleus is filled with large and small globules of heterochromatin, not obviously related in size or number to the chromosomes. Among the epidermal cells some can be distinguished as having a greater amount of cytoplasm. In such cells at a later stage (fig. 3) the cytoplasm is seen protruding in an amoeboid fashion. A similar type of epidermal cell in *P. australis* shows a slightly different appearance of heterochromatin. There definite chromatin bodies are observed but a large amount of chromatin material is seen dispersed throughout the nucleus. Some of the epidermal cells, although not having an enlarged nucleus, show a characteristically larger amount of cytoplasm, and consequently a greater cell surface. Such a stage, seen in figure 2, corresponds to the bulb-like stages seen in figure 1.

From this stage on, the cell wall has pseudopodium-like processes and the nucleus enlarges (fig. 4). The nucleus contains about the same number of heterochromatic bodies but they are greatly enlarged. The response of these bodies to the Feulgen reaction is as deep as that of the heterochromatic bodies in the epidermal cells, but occasionally vacuoles can be seen in the largest ones. In the photomicrographs that follow, it is possible to observe an enormous increase in the amount of cytoplasm and of chromatin. The nucleolus also enlarges during this process. This can be seen by comparing the nucleolus which appears as a grey body in one of the small epidermal cells (fig. 8) with that, in a developing trichome (fig. 7) at a stage similar to that in figure 6.

The further increase in size of the entire trichome cell cannot be illustrated at the same magnification. An epidermal cell with an original length of about 10 μ becomes a unicellular structure 450–750 μ in diameter.

In most trichomes when a certain size is reached the increase in amount of chromatin within the nucleus stops. The heterochromatic bodies become vacuolated and do not stain so deeply with the Feulgen reaction as they did at earlier stages. Further changes in the nucleus then take place. It is often possible to see in sectioned material a fully developed trichome containing somewhere in the stalk region the remains of the nucleus in form of a lobed body which no longer responds to the Feulgen reaction.

It is almost impossible to determine at what stage of trichome development the deterioration of the nucleus takes place, but it is evident by the time the characteristic thickenings appear on the cell wall. The fully formed



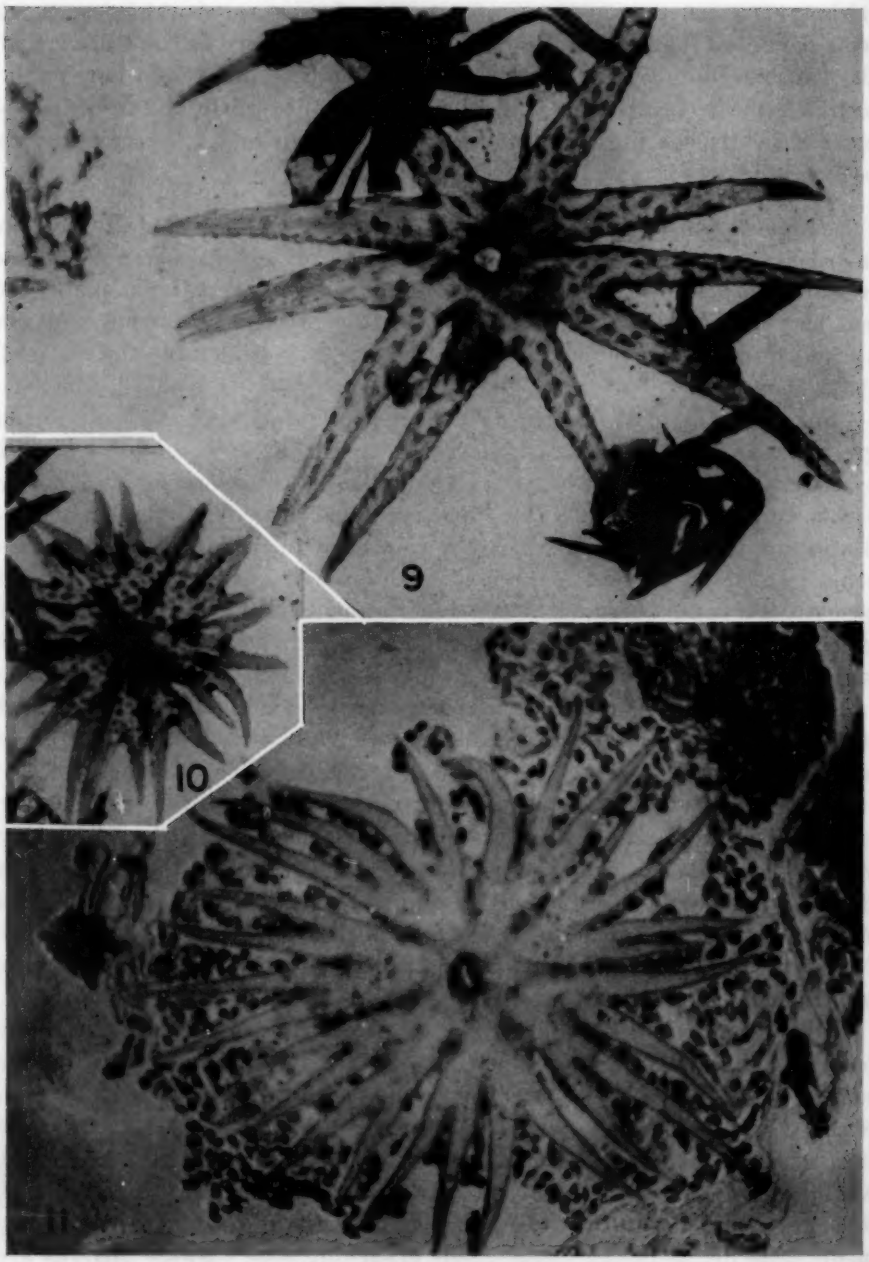
FIGS. 6–8. Leaf smears from adult specimens of *Physaria Geyeri* stained by Feulgen reaction and light green. All × 1960. FIG. 6. Full view of developing trichome. FIG. 7. Nucleus of a developing trichome showing enlarged heterochromatic bodies and nucleolus. FIG. 8. Epidermal cell showing small nucleolus and heterochromatic bodies.

trichome is a structure consisting of cell wall, the surface of which is covered with elevations such as are visible on a trichome in figure 1. The full view of the trichome branches in *P. Geyeri* after complete differentiation can be seen in a smear (fig. 9). This is the final stage in the growth and the development of the trichome. Similar stages for *P. australis* and *L. Sherwoodii* can be seen in figures 10 and 11.

Morphology of Adult Trichomes. This study was initially undertaken in order to compare the general appearance of fully differentiated trichomes in stained smear preparations, herbarium specimens, and living plants. It was necessary to find out whether or not the process of fixation and the hydrolysis preceding the Feulgen reaction altered considerably the shape of the trichomes.

For the study of the living material the following were available in the greenhouse: 4 specimens of *P. Geyeri*, 1 specimen of *P. australis*, and 4 specimens of *L. Sherwoodii*. A few older and younger leaves and flower shoots were taken from each plant and examined immediately under magnification of 125×. It has been noticed that only fully developed trichomes could be studied by this method, since the earlier stages were obliterated beneath the dense covering of trichome branches. In *P. Geyeri*, leaves of greenish and silvery color were observed, but regardless of color the upper surface of the leaves was covered with dense trichomes, apparently uniform in size. The lower surface of the leaves was covered with fully differentiated trichomes much smaller in size. The elongated basal portion of the leaf blade was the area most densely covered with trichomes. The branches of the trichomes in a living plant were uniformly straight and were not bent or twisted. The thickenings on the wall of the trichome branches were clearly visible. The trichomes were spaced so as to permit counting the branches on the individual trichomes. From 50 counts taken from the leaves with a silvery coloring the number of trichome branches varied from 9 to 17, while from 50 counts from leaves with a greenish coloring the number of branches per trichome varied from 7 to 12.

The trichomes appeared to be nearly uniform in circumference. The pattern in trichome branching was not uniform. Observation of the upper surface of the leaf with the trichomes undisturbed in their natural position revealed nine basic recurring patterns in the branching of trichomes. Few trichomes were symmetrical. Radiating branches on the individual trichomes were not of uniform length. Frequently one branch was exceptionally long. Such long branches did not always arise from the central region but commonly were derived from dichotomous branching. The various patterns are represented by diagrammatic drawings (fig. 12) in which the relative length and position of the trichome branches are shown. The lines represent a



FIGS. 9–11. Fully developed trichomes as seen in leaf smears stained by Feulgen reaction and light green. All × 200. FIG. 9. Trichome of *Physaria Geyeri*. FIG. 10. Trichome of *Lesquerella Sherwoodii*. FIG. 11. Trichome of *Physaria australis*.

hypothetical midline for each trichome branch starting at the center of the basal region of the branch and ending at the distal end. It can be noticed that dichotomous branching occurs in many branches. Pattern *A* was rather unusual and not so frequently found as the others. In this pattern dichotomous branching does not arise until after a certain development from the base of the original four radiating branches. Pattern *B* shows a similar arrangement except that one original branch never divides dichotomously. Pattern *C*, *D*, and *G* show one disproportionally long arm. In pattern *D* there is almost no clear-cut dichotomous branching. A secondary dichotomous branching can be seen in pattern *H*.

Four specimens of *L. Sherwoodii* were available and several leaves were taken from each plant. The color of the leaves varied from silvery green to green as in *P. Geyeri*. The trichomes, however, appeared smaller in *L. Sherwoodii* than in *P. Geyeri*, but were more compact and more nearly peltate, with the central region larger than in *P. Geyeri*. The branches of the individual trichomes were not located in the same plane. This made counts and pattern-determination difficult. The number of branches encountered on individual trichomes was 13, 14, and 15. The counts did not essentially differ on the upper and the lower surfaces of the leaf. In *L. Sherwoodii* most radiating branches divide dichotomously and there are few single branches arising from the central region. There has been some difficulty in establishing the most frequent patterns in *L. Sherwoodii*, but the following two were most commonly encountered. Pattern *J* showed the arrangement in a 14-branched trichome. Four main branches divide dichotomously at some distance from the center while 3 other main branches evidently divide at the very center. In pattern *K* also of 14 branches, each of the 7 main branches divides at some distance from the center, but the whole trichome is not perfectly radially symmetrical.

The observed leaves of *P. australis* were all from the same plant, silvery green in color. The trichomes appeared larger than those of *P. Geyeri* and *L. Sherwoodii*. The dense pubescence made the counts of trichome branches difficult. The number of branches on individual trichomes was seldom lower than 20. The branches of each trichome extended in more than one plane. In stained preparations the shape of such trichomes was altered by pressing all the branches into one surface. The branches were more uniform in length than in the two other species. Thus the outline of the trichome appeared circular. In this species, as in *L. Sherwoodii*, it was difficult to determine trichome patterns. A pattern with 27 branches was seen quite frequently. In this type of trichome, as shown in pattern *L*, there are seven main branches with a primary and secondary dichotomous branching. The failure of one branch to divide results in the total of 27 instead of 28 branches.

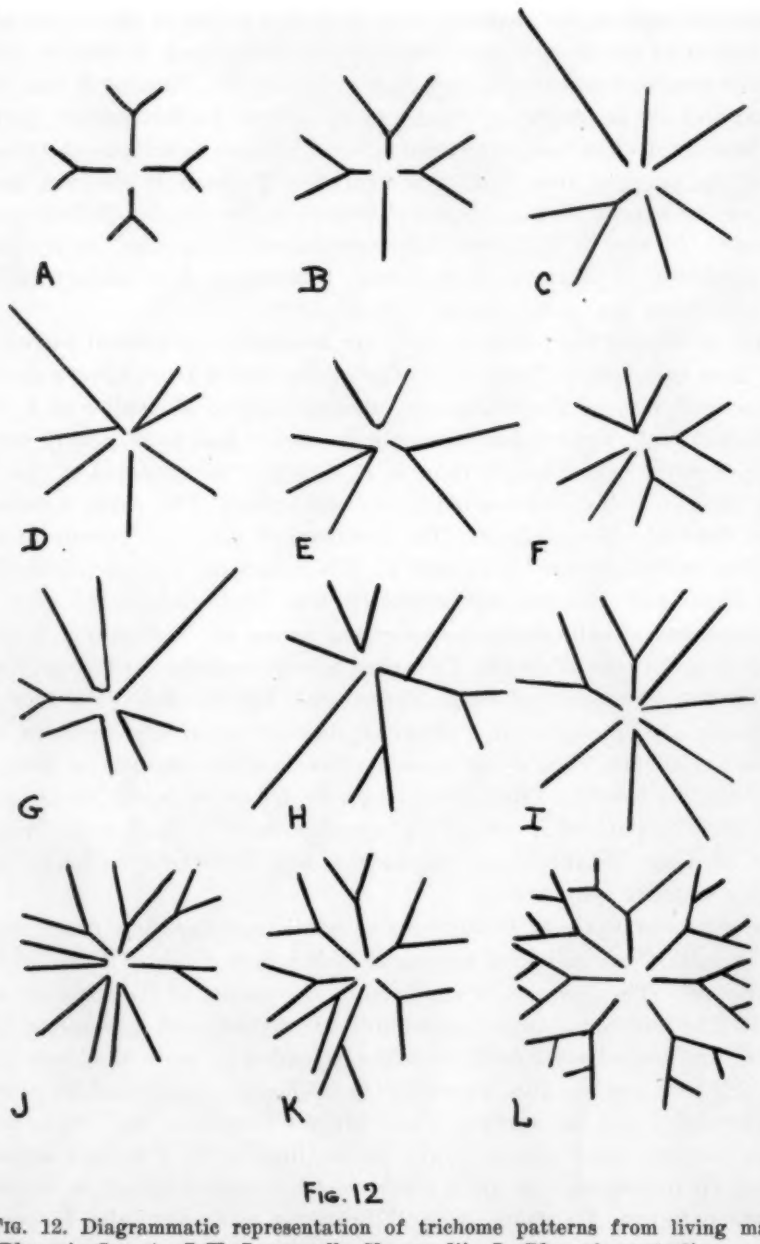


FIG. 12

FIG. 12. Diagrammatic representation of trichome patterns from living material. A–I, *Physaria Geyeri*. J–K, *Lesquerella Sherwoodii*. L, *Physaria australis*.

Nine specimens of *P. Geyeri* Gray and ten specimens of *L. Sherwoodii* Peck from the herbarium of the New York Botanical Garden were studied under a 9x ocular and a 4.8x objective.

It was observed that dried trichomes were essentially identical in shape with those of the living plants. In *L. Sherwoodii* trichomes were very dense on the upper portion of the leaf and on the leaf blade, but less dense on the flower-bearing shoots. The trichomes were translucent. The number of branches observed on individual trichomes varied between 8 (10) and 17. Similar observations on the distribution of trichomes were made in *P. Geyeri*. The number of branches on individual trichomes varied between 8 and 12. It appeared from the observation on these few herbarium specimens that the size of trichomes varies from plant to plant, probably with the age, and on the plants with larger trichomes the number of branches on individual trichomes appeared to be higher. The counting of branches on the individual trichomes was difficult because of their proximity.

The stained preparations provided material for a more detailed study of fully developed trichomes. As was shown in figure 1, fully developed trichomes can be already found on the young leaves of 6-weeks-old plants. They were previously described as the final stage in development and differentiation. The fully developed trichomes of the three species can be compared in figures 9, 10, and 11. These trichomes were chosen at random from the stained smeared preparations and are shown with the same magnification. Thus only the surface view of the radiating branches can be seen. The trichome of *P. Geyeri* shows thickenings on the wall characteristic of the fully differentiated trichome. The branches all lie in the same plane. The trichome of *L. Sherwoodii* exhibits the same thickenings on a relatively higher number of branches. The diameter of the entire trichome appears however much smaller. Apparently the several branches which in the natural condition lie in different planes have been compressed into one plane by the smear technique, giving the trichome an artificially enlarged central region which imitates the shield of a peltate trichome. The trichome of *P. australis* is not shown in perfect focus. This was done in order to emphasize the difference between this giant differentiated cell and the epidermal cells, one of which gave rise to it. The surface of the branches is covered by the same kind of thickenings. In the center the opening caused by tearing off the trichome stalk can be observed. The trichome appears to be the same size as that of *P. Geyeri* but it has a much larger number of branches. These branches are not like those of *P. Geyeri* and are apparently compressed into one plane by the smear method.

It has been a question whether or not to consider these photographs as representative of the trichomes of the three species under study. It has been revealed by previous study of the living and herbarium material that there

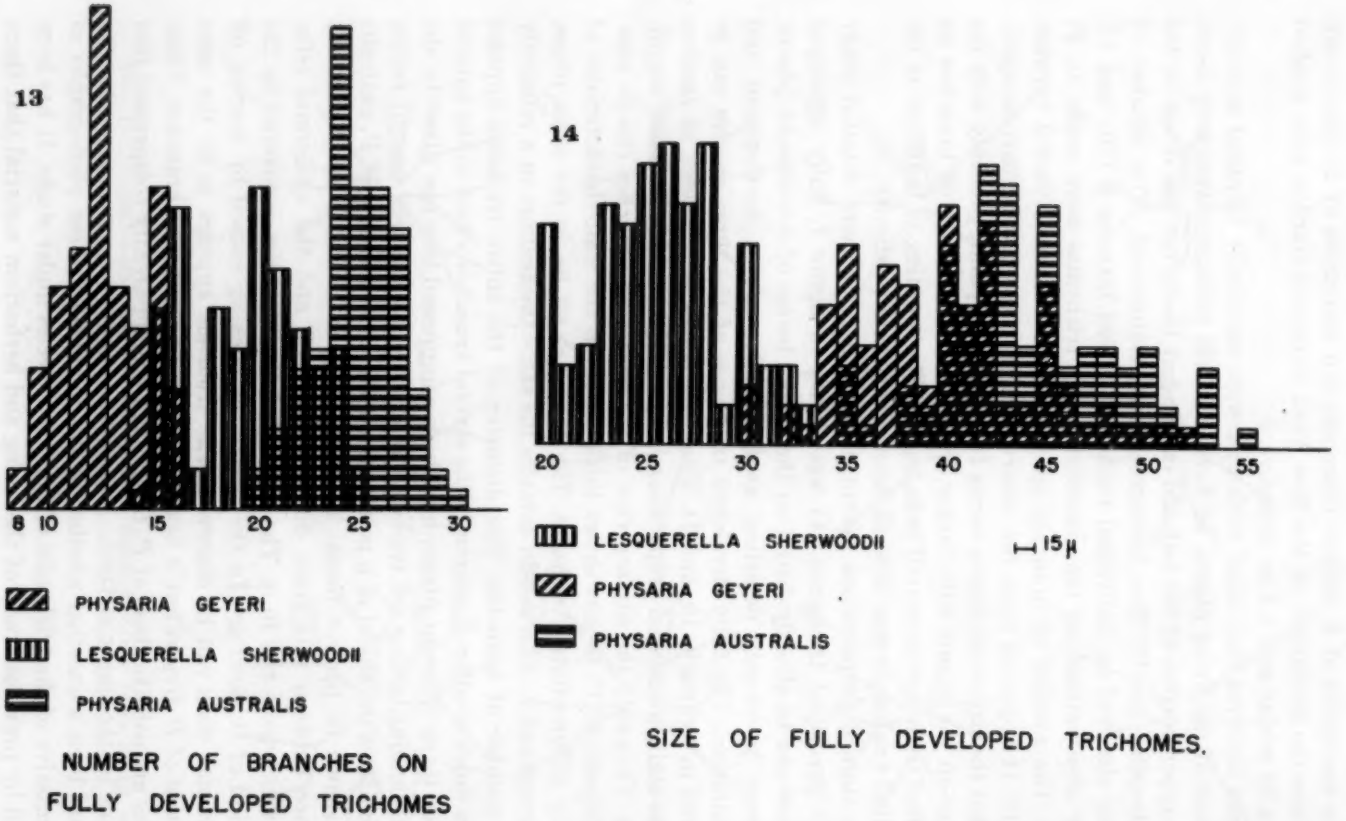


FIG. 13. Histogram representing the distribution of the number of branches on fully developed trichomes of *Physaria Geyeri, Physaria australis* and *Lesquerella Sherwoodii*. FIG. 14. Histogram representing the variation in size of fully developed trichomes of *Physaria Geyeri, Physaria australis* and *Lesquerella Sherwoodii*.

seems to be great variability in size of the trichomes and in the number of branches on the individual trichomes within the species. For this reason it was proposed to investigate further, although again on a limited number of plants, the sizes and the number of branches of the trichomes.

From previous studies on living and herbarium specimens it was observed that there was no number of trichome branches characteristic for each species. One hundred trichomes from 10 different slides taken from various specimens were examined for each of the three species. No general conclusions are attempted. It is possible, however, to state that in the three samples the numbers of branches of the individual trichomes are distributed within three different ranges. In 100 trichomes of *P. Geyeri* which were examined, the number of branches varied from 8 to 16. Twenty-five trichomes out of this sample of 100 had 12 branches. In *L. Sherwoodii* the number of branches varied from 14 to 25 and in *P. australis* from 20 to 30. These results are seen in figure 13.

While examining slides of Feulgen-stained material one easily forms the impression that it is possible to distinguish between the material from the three species by trichomes alone. It seems that in general the trichomes of *P. Geyeri* have fewer branches, those of *P. australis* have more numerous branches, and those of *L. Sherwoodii*, although with numerous branches, can be distinguished by the condition of the prochromosomes in the neighboring epidermal cells and by the trichome size. The different appearance of the prochromosomes will be described elsewhere. The size of the trichomes in the three species has been studied from the stained specimens. The measurements were taken by choosing the maximum trichome diameter from tip to tip of the opposite branches. From the plotted results (fig. 14) it appears that the values for *L. Sherwoodii* are much lower than for either *P. Geyeri* or *P. australis*. Thus the general impression that the trichomes in the available specimens of *L. Sherwoodii* are smaller seems to be corroborated by these data, although this statement cannot be validly made about the trichomes of *L. Sherwoodii* in general.

Discussion. There seems to be no disagreement, among the authors who described the development of trichomes, as to the cells from which the trichomes originate. The process by which unicellular stellate trichomes described in the present paper grow and differentiate is more striking, however, than most cases in which a more complex multicellular epidermal hair forms by repeated cell divisions. The trichomes of *Physaria* and *Lesquerella* here described arise from epidermal cells which apparently in the initial stages do not differ from the other epidermal cells. The first sign of their differentiation is the increase in the amount of cytoplasm and most of the growth takes place when the cell nucleus and cytoplasm appear normal.

FIG. 14. Histogram representing the variation in size of fully developed trichomes of *Physaria Geyeri*, *Physaria australis* and *Lesquerella Sherwoodii*.

Whatever the forces are that influence some of the epidermal cells to increase their volume and surface to such great extent and to undergo such profound changes in the cell shape they do act selectively on certain cells. In the sections of *Lesquerella* and *Physaria,* trichomes have never been found arising from adjacent epidermal cells, although the plants have an abundant pubescence.

In the process of differentiation of the stellate trichomes it was observed that the cell fails to undergo mitosis, although the cell surface increases rapidly. Even more spectacular is the increase in the amount of chromatin within the nucleus of the trichomes. The resting condition of the nucleus in *Lesquerella* and *Physaria* is characterized by massive heterochromatic bodies. The chromatin in *P. Geyeri* and in *L. Sherwoodii* is condensed in more definite bodies than that of *P. australis,* the nucleus of which contains large amounts of chromatin distributed throughout in form of minute granules. Studies on the heterochromatin are in progress. The increase in amount of chromatin during the development of trichomes can be judged from the increased size of the nucleus and of the individual prochromosomes. The heterochromatic bodies in the very young trichomes respond as intensely to the Feulgen reaction as do the large ones in a nearly differentiated trichome. There is apparently not sufficient vacuolation of the heterochromatic bodies to account for such enormous increase in size. There seems to be no "dilution" of chromatin within an enlarged prochromosome-like matrix. It seems that the size increase in the nucleus of a developing trichome is verifiable. The nucleus remains in the resting stage while the cell growth takes place. This suggests that within this resting nucleus chromatin reduplication takes place. It is difficult to judge whether or not at the final stage the cell reached a high degree of polyploidy. If the size of the nucleolus were a reliable feature by which to determine polyploidy, the view that trichomes become polyploid during their development could be supported by actual evidence (figs. 7, 8). As was previously stated, the nucleus of a differentiating trichome remains in the resting condition. It maintains its position near the center of the stellate structure, slightly below the upper surface of the stalk region, while undergoing an increase in size. At the same time the cell attains an enormous size by extrusion of pseudopodium-like processes, which are referred to as trichome branches in the present paper. In the initial stages of development the cytoplasm fills the entire cell and its branches. The vacuole is relatively small. As the branches of the trichome elongate and become more numerous, a larger vacuole appears and the cytoplasm coats only the inner portions of the trichome walls in a thin layer. The cytoplasm thus increases in amount up to a definite limit. This probably occurs before the cell wall and the nucleus complete their growth.

During the process of branch formation the trichome can be considered

an elongating cell so long as the nucleus, which increases in size, retains a normal appearance. Until such a state is realized, it might be possible to arrest thhe process by preventing differentiation, which is accompanied by disintegration of the nucleus and the thickening of the cell wall. Before the irreversible nuclear changes take place, it might be possible to stimulate nuclear division in the fairly large trichome as was possible for elongated cells of *Allium cepa* by chemical treatment (Berger 1946). In such a case the suspected polyploidy of the trichome might be revealed even if the actual cell division failed.

One might be inclined to believe on the basis of the observations made that in trichomes of the three species the actual growth can be influenced independently of the process of differentiation. In the herbarium specimens consisting of adult plants, fully differentiated trichomes of much smaller size could be occasionally seen among the larger ones, but most of these were limited to certain regions such as the basal elongated portion of the leaf blade and the lower surface of the leaf. Wherever such small trichomes were found in the smear preparations, it could be noticed that the pseudopodium-like branches arose in cells with a smaller amount of cytoplasm. The nucleus in such cells has not the ratio to the cytoplasm that exists in larger trichomes. Thus it seems that in cells giving rise to smaller trichomes, the differentiation is speeded up, taking place at an earlier stage, and the period of growth is shortened. If one considers that at the time the trichome becomes differentiated and its nucleus deteriorates the sister epidermal cells have nuclei which are able to undergo mitosis, one is impressed by the fact that cells of apparently the same origin are endowed with different growth habits and life spans.

Rosenvinge (1911) noticed that in the marine algae the trichomes deteriorate long before the plants die in autumn. This probably occurred because dead structures consisting of cell wall, non-functional nucleus, and dead cytoplasm could not resist the influence of salt water in which they were immersed. In land plants in a rather arid habitat the trichomes are well preserved long after the cell division in the leaves have stopped. Still the life span of a trichome is undoubtedly shorter than that of the epidermal cells.

It is difficult in the present study to draw any quantitative conclusions on the increase in volume of the cell relative to the increase in volume of the nucleus. If one considers in *P. Geyeri* the diameter of smallest epidermal cell nucleolus as 4 units in respect to 10 units of nucleolar diameter in a trichome at a late stage, as seen in figures 8 and 7, the increase in volume could be expressed as a ratio 8 : 125 or as 1 : 16. The diameters of the nuclei in the same cells would be relatively equal to 10 and 30 units, and thus the relative nuclear volumes would be in the ratio of 1000 : 27000 or 1 : 27. If

the cell volumes are considered, there are even greater difficulties than those connected with the arbitrary choice of cells the nuclei and nucleoli of which must be considered roughly as spheres. The main difficulty in the arbitrary choice of adult trichome is the observed variability in number of branches.

From a study of a few available living and herbarium specimens, including the Feulgen smear preparations, it is hardly possible to make any generalizations on the relationships between the three species on the basis of trichome size, form, and other features. This would require a survey of a large number of plants. It appears however that the plants of each species showed uniform variability in trichome size and number of branches on individual trichomes. It also appears from the bimodal distribution that dichotomous branching plays an important role in the determination of the number of branches on individual trichomes. The various patterns observed on the same leaf seem to make the task of differentiation of species by trichome shape an impossible one. These patterns were reported as most numerous for *P. Geyeri*. It is possible that an equally large number of patterns can be found in *L. Sherwoodii* and in *P. australis* but it is more difficult to determine this because of the large number of branches on individual trichomes. The distribution zones in the number of branches on individual trichomes and in trichome sizes suggest that these two features of the trichomes might be of some help in the taxonomical studies of these two genera of cruciferous plants.

SUMMARY

1. Unicellular stellate trichomes in *Physaria Geyeri, Physaria australis,* and *Lesquerella Sherwoodii* have been studied in Feulgen-stained smear preparations and in sections, as well as in living and herbarium material.

2. The process of trichome development has been followed in the three species and described in detail for *Physaria Geyeri*. In the latter during the process of trichome differentiation from epidermal cells, the volume of the entire cell as well as of the nucleus, nucleolus, and individual heterochromatic bodies increases considerably. As a result of this process an epidermal cell about 10 μ in length becomes a stellate unicellular structure 450–750 μ in diameter. The average final nuclear volume in *P. Geyeri* is 27 times that of the initial nuclear volume and that of the nucleolus approximately 16 times the initial nucleolar volume. It is difficult however to judge whether or not at the final stage the cell reaches a high degree of polyploidy, although the amount of chromatin within the nucleus increases while the nucleus remains in a resting condition.

3. Fully grown trichomes consist of numerous branches varying in number from 8 to 16 in *P. Geyeri*, from 14 to 25 in *L. Sherwoodii*, and from 20

to 30 for *P. australis*. The adult trichomes of *Lesquerella* are smaller than those of either *P. Geyeri* or *P. australis*. Several patterns of trichome branching have been observed for each species.

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BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 76, No. 3, pp. 196–209 MAY 1949

THE GENUS ALFAROA

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Alfaroa, described from Costa Rica by Standley (1927a), is one of the most interesting genera in the Juglandaceae.

Intensive studies by the writer on the inflorescences, pistillate flowers, and staminate flowers (Manning 1938a, 1938b, 1940, 1948) of all members of the family including *Alfaroa* have shown that part of the description by Standley was inaccurate and incomplete. Furthermore, recent collections made for the writer by Dr. Alexander Skutch have furnished a more complete knowledge of the staminate inflorescences and the internal structure of the fruit. This genus is one of the most primitive members of the family, as shown by studies by the writer and by Heimsch and Wetmore (1939). For these reasons it seems necessary to give a corrected description of its flowers, fruit, and other features, with a discussion of its relationships.

A few paragraphs from the letters of Dr. Skutch are of significance:

"... Upon receiving your renewed inquiry about *Alfaroa*, I found a single sterile specimen here in the museum, identified by Standley. Then I recalled that at Vara Blanca I had seen a small tree of that appearance. In June or July it bore unripe fruits. ..." Recalling these facts, I thought it worth while to return to my old collecting ground for another look. Passing through the woods, I had the good luck to stumble upon a flowering tree which had just been felled for lumber and was still fresh. The foliage of this lofty tree was so different from that of the specimen of *Alfaroa* I had examined that at first I thought it must belong to a distinct species, possibly an undescribed species of the Juglandaceae. Certainly but for the chance of running into this fallen tree, I would not have collected material from the lofty and difficult trees of this appearance as *Alfaroa costaricensis*. But later, examining other individuals, I connected this one with the specimen in the museum, which evidently came from a young tree or a stump sprout. Stump sprouts bear young shoots and foliage with prominent long pubescence; the leaves of mature trees are nearly glabrous. The numerous leaflets on the leaves of stump sprouts are acute and conspicuously dentate; old trees have fewer leaflets to the leaf and these are blunt at the apex and sparingly if at all dentate. The herbarium specimens I have for you show these differences quite clearly. They also show that the leaves are sometimes borne three at a node.

"As I was returning from what I considered a successful trip, I found a large fallen branch of *Alfaroa* lying beside the road. It bore numerous long staminate catkins in liberal clusters; there was no pistillate inflorescence among them. This heavy branch broke from a great tree at least one hundred feet high and about three feet in diameter at breast height, where the trunk was deeply furrowed and ridged. Examining the lofty crown through my binoculars, I could see no pistillate inflorescences; but because of the great height of the tree this negative evidence is possibly not conclusive.

[1] The writer wishes to express appreciation to the curators of the herbarium at the Chicago Museum of Natural History and of the U. S. National Herbarium for their generosity in lending specimens. The drawings were made by Grace A. Petersen and Donald C. Baird, Jr.

I think it probable, however, that *Alfaroa* is polygamo-dioecious. The predominantly pistillate trees bear small staminate aments at the bases of some of the pistillate spikes, as stated in the original description of the genus; but there are also trees (or at least branches) which bear large clusters of far longer staminate aments and no pistillate flowers.

"The region where these collections were made is the northern slope of the Cordillera Central between the volcanoes Poas and Barba. Here *Alfaroa* is a common tree between 5000 and 6000 feet above sea level; it attains a height of 80 to 100 feet and possibly more, with trunks two to three feet in diameter. The bark is fairly smooth and varies from light gray to light brown in color. The crown is spreading, with dense compact foliage. It is very beautiful when putting forth new leaves with a delicate light red tint. No one whom I questioned had heard of the name "gaulín." I was given the name "uruca"; but this more properly refers to *Trichilia*. . . ."

"The pistillate spikes are erect; the short staminate catkins stand out from their base. The long staminate catkins from collection 4685 were already so withered when I found them that I can make no definite statement as to their attitude. I should judge they must droop. . . ."

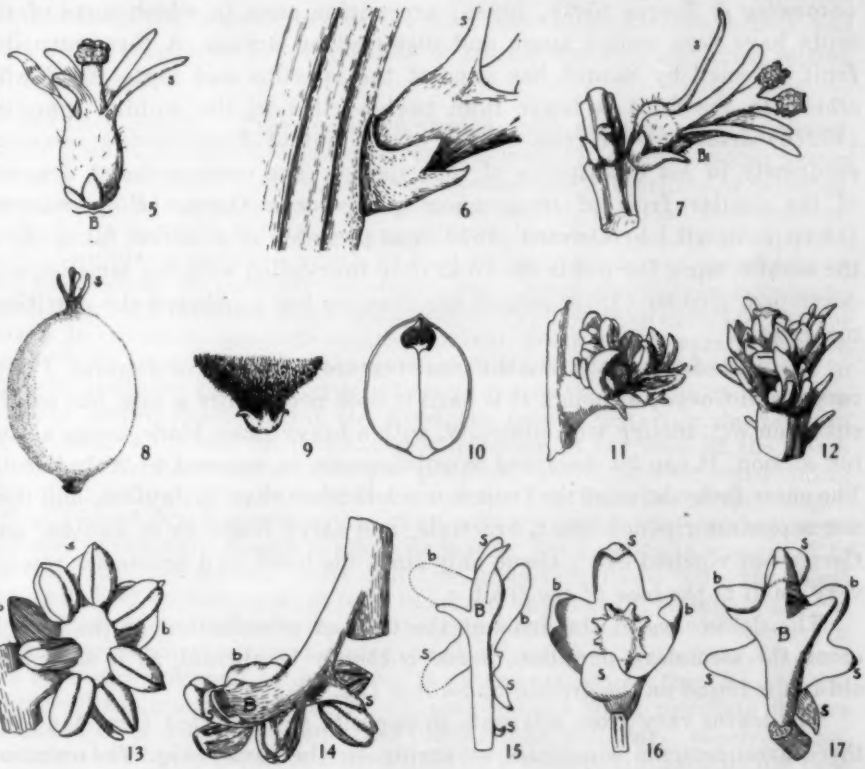
"As the specimens from tree 4684 show, the flowers rise above old leaves much damaged by insects. Since I selected the flowering twigs which bore the best foliage, the majority of the catkins were associated with leaves still more badly worn; hence they arise (on this tree at least) from the t[illegible]s of old shoots of the previous year. They are terminal (not on lateral spurs) on strong twigs at the very top of the tree. . . ."

Standley (1927a) describes the staminate flowers as "few, solitary and sessile at the base of the (pistillate) spike or few (2 to 4) and arranged upon two short basal branches." The writer, in his study of the inflorescences (Manning 1938a) stated of the inflorescences of *Alfaroa*, "If the flowers are wind pollinated, as seems probable, the number of staminate flowers is very small, and it is possible that individual branches or individual trees may produce longer staminate catkins. Such catkins have not as yet been found." Skutch has now found such catkins, and it is evident that there are several different combinations of staminate inflorescences.

There are three types of staminate branches which may occur at the base of the pistillate spike: one-flowered, few-flowered, and many-flowered (figs. 2, 3, 11, 12). Furthermore, in some cases the two kinds of flowers may be distinct, the pistillate spikes and the panicles of elongate staminate catkins occurring on separate twigs of the same tree (fig. 3), or on different trees (fig. 1). It is interesting to note from figure 1 that on one twig most transitional stages in position of the staminate panicles can be found from a characteristic terminal position at the tip of a main leafy shoot to a position at the tip of a rather short essentially leafless branch on the old wood, the latter inflorescences thus appearing short-stalked and axillary, similar to the condition in *Engelhardtia pterocarpa* and *E. spicata*, and approaching the conditions in *Pterocarya*, *Juglans*, and *Carya*. Such stages, transitional from ancestral terminal positions to advanced axillary positions were proposed in the article on inflorescences (Manning 1938 a) as necessary theoretical ancestral intermediates, and they have now been found in one modern species.

FIG. 1. *Alfaroa costaricensis* Standley var. *elongata* Manning, var. nov.; *Skutch 4685*, staminate flowers only; complete catkins of only one panicle drawn, tips of others cut off; panicles terminal on new growth, and in some cases essentially axillary on old growth ×¾. FIGS. 2–4. *Alfaroa costaricensis* Standley ×¾. FIG. 2. *Standley 33620* (TYPE) showing short staminate branches. FIG. 3. Preserved material, collected by Skutch (presumably his *4684*), showing panicle of elongate staminate catkins and androgynous panicle (pistillate and staminate catkins) on adjacent branchlets. FIG. 4. Portion of twig with leaf; *Skutch 4684*.

The internal structure of the fruit was not fully understood by Standley. Better material of *Alfaroa costaricensis* and more detailed study of *Engelhardtia pterocarpa* and *E. mexicana* show that in internal structure of the fruit these three are practically identical. The fruit (figs. 8–10, 18–23) is eight-celled in the middle, owing to the presence of primary, secondary,



FIGS. 5–15. *Alfaroa costaricensis* Standley. FIGS. 16, 17. *Alfaroa costaricensis* var. *elongata* Manning. B, bract; B1, central lobe of bract; b, b, bracteoles; s, sepal. FIGS. 5, 7. Pistillate flowers; *Standley 33620*. FIG. 5. The unusual type of flower with 5 sepals, front view. FIG. 7. The usual type, side view. FIG. 6. Base of pistillate flower, side view, much enlarged (*Skutch 4684*), showing the bracteole rim. FIG. 8. Fruit. × 1. FIG. 9. Base of fruit, enlarged. FIG. 10. One valve of nut, showing the small common cavity of the loculus. FIGS. 11, 12. One-flowered staminate branches, without and with central abortive pistil; *Standley 33620*. × 5. FIGS. 13, 14. Staminate flowers stalked, with round receptacles; *Skutch 4684*. FIG. 15. Staminate flower; *Standley 33620*. FIGS. 16, 17. Staminate flowers, sessile with elongate receptacles; *Skutch 4685*.

and tertiary septa. In addition to these there are plate-like outgrowths, lamellae, from the secondary and tertiary septa, these sometimes T-shaped at the ends, thus making the internal structure quite complex—incompletely sixteen-celled; the lamellae disappear toward the base of the fruits. The

tertiaries disappear above, so that the nut is four-celled just below the one-celled apex; the tertiaries may also be lacking at the very base in those fruits of *Alfaroa* which have tapering bases. Some of the septa or lamellae may be lacking or fused with other septa, so that the internal structure is not uniform in all nuts. The fruits of *Alfaroa* found in most herbaria (*Standley & Torres 50870, 50986*) are unripe ones, in which some of the septa have been pulled apart and distorted by drying. A three-carpelled fruit collected by Skutch has some of the lamellae and septa fused with others, so the fruit is fewer than twelve-celled in the middle. Standley (1927b) described the cross section of the nut of *Engelhardtia mexicana* accurately in his description of that species. The cross-sectional drawing of the similar fruit of *Oreamunoa*[2] *peterocarpa* Oerst. [*E. pterocarpa* (Oerst.) Standl.] by Oersted (1870) was probably of a section taken above the middle, since the nut is shown as only four-celled with the lamellae well developed. Eichler (1878) copied the drawing but numbered the partitions incorrectly.

The wall of the nut is of a different texture from that of *Juglans*, *Pterocarya*, and *Carya;* although it is hard it does not require a saw, but can be cut when wet, though with difficulty, with a heavy razor blade, using a sawing motion. It can be described as subligneous, as opposed to truly woody. The outer fleshy layer of the fruit is much thinner than in *Juglans*, and does not represent ripened bract, bracteole, and calyx tissue as in *Juglans* and *Carya*, but ripened calyx tissue only since the bract and bracteoles remain very small at the base of the fruit.

The dehiscence of the fruit at the time of germination of the seed is along the secondary partition, hence is clearly loculicidal, as is shown by old fruits found on the ground by Skutch (fig. 10).

The leaves vary from alternate to opposite and whorled (figs. 1–4), all three arrangements sometimes occurring on the same twig. The common arrangement seems to be opposite.

As the writer stated in a previous article (Manning 1940) the bracteoles appear absent from the pistillate flower. In some flowers of the abundant preserved material collected by Skutch, there is a minute bracteolar rim around the base of the ovary connected with the side lobes of the bract (fig. 6). In most flowers this rim is buried in the axis of the catkin. The pres-

[2] It is necessary to stabilize the spelling of the generic, sectional, and specific name, *Oreamunoa*. Four different spellings occur in literature. The genus was dedicated by Oersted (1856) to Don Francisco Maria Oreamuno. Unfortunately, in the original description of the genus, Oersted spelled the name of the Costa Rican statesman Oreomunna, and called the genus *Oreomunnea*. Oersted in a book dedicated to Oreamuno in 1863 correctly spelled the latter's name, and in an article on the Juglandaceae in 1870 changed without comment his own spelling of the genus to *Oreamunoa*.

ence of this bracteolar rim shows the relationship to *Engelhardtia* and other genera. Bracteoles are present in the staminate flowers.

Figures 5–7, 11–17 show the pistillate and staminate flowers. Other floral drawings are given in the papers of the writer cited above.

A corrected description of the genus *Alfaroa* is here given (most of the changes from the original are in the staminate inflorescences, bracts and calyx of the staminate flower, position of stigma, embryo, and cross section of the fruit).

ALFAROA Standl. Trees or large shrubs; pith solid; buds superposed, closely glandular-dotted, (naked or valvate-scaly?), often hirsute; leaves probably deciduous(?), mostly opposite, occasionally alternate or whorled, estipulate, pinnate, with no truly terminal leaflet, the leaflets numerous, alternate or opposite, serrate on young trees, entire or nearly so on older trees, glandular-punctate beneath at least on younger leaves, membranaceous; monoecious or partially dioecious, some trees exclusively staminate, others with both pistillate and staminate flowers; flowers in spikes or catkins usually in panicles; pistillate spikes terminal, erect, the flowers numerous, about 30–50, inserted singly, closely sessile; staminate catkins clustered in separate drooping panicles terminal on new growth and also on short essentially leafless shoots on the old wood, the lateral flowering shoots often superposed, or the catkins forming side branches at the base of the pistillate spikes, the staminate catkins and pistillate spikes together constituting a terminal androgynous panicle, the staminate side branches often reduced to 2 or 4 short few-flowered spikes or to solitary apparently sessile flowers or absent; staminate flowers stalked or sessile, the receptacle elongated to nearly round, the 3-lobed bract and two bracteoles fused with the floral receptacle and appearing as part of the floral envelope; true sepals 4, 3, or 2, oblong, obtuse, variable in size and arrangement; stamens 6–10 inserted in a single series about a naked center, or occasionally in the solitary flowers with an ovoid rudiment of an ovary, the filaments nearly obsolete, the anthers 2-celled, glabrous, dehiscent by longitudinal slits; pistillate flowers subtended by a minute 3-lobed bract shorter than the ovary, bracteoles apparently absent or sometimes represented by a minute rim around the base of the ovary, the calyx deeply 4- or rarely 5-lobed, the lobes oblong-linear, as long as the style and stigmas, unequal, obtuse, erect, persistent upon the apex of the fruit, the style shorter than the perianth lobes, bifurcate, the 2 (rarely 3) stigmas carinal, median, subglobose, the verrucose stigmatic areas on the outside of the style branches or covering the tips; fruit oval or obovoid, about 2.5 cm. long, with neither husk nor wings, the skin (probably modified calyx) nearly dry, papery-thin, hairy, indehiscent, adhering closely to the nut proper, the bract a scale at the base of the fruit; nut proper neither ridged nor rugose, with coriaceous-subligneous thin walls, falsely 8-celled, with nearly complete primary, secondary, and tertiary septa, the secondary and tertiary with lamellae projecting into the loculus, 8-celled in the lower half, 4-celled near the apex, 1-celled at the very top; seed 8-lobed, 4-lobed, and entire, following the lobes of the loculus, the lobes of the embryo averaging 1 mm. thick, each cotyledon probably 4-lobed, one cotyledon in each valve (not carpel) of the nut, the cotyledons apparently separate from each

other (so lobes of different cotyledons not entangled together); nature of the seedling as yet unknown; nut at time of germination of the seed loculicidally dehiscent, the valves lateral to the axis.

Standley (1927a) gives a complete description of the single species, *A. costaricensis* Standley; this is accurate except for the staminate inflorescences. The distribution is given there and in the *Flora of Costa Rica* (Standley 1937) for that country. In general, *Alfaroa,* known locally in Costa Rica as *gaulin, gavillancillo,* or *uruca,* is common in central Costa Rica in forests near Cartago at an elevation of 1250–1800 meters, in western and central Guatemala, and in western Panama. The following are the definite localities recorded in herbarium material for the typical species.

COSTA RICA: El Muñeco, south of Navarro on the Rio Navarro: *Standley 1925* (CM), *Standley 33501* (US, AA), *33504* (US), *33620* (US, TYPE), *Standley & Torres 50870* (US, AA, CM, GH), *50874* (US), *50986* (US), *51078* (US), *51204* (US), *Stork 2691* (US, CM); La Estrella: *Standley 39217* (US); Alto de la Estrella: *Standley 39122* (US); Juan Vinas: *Lankaster 1922* (US); Santa Clara de Cartago: *Lankaster 1929* (CM); Santa Maria Dota: *Stork 1700* (CM); Turrialba: *Dita Keith 371* (CM); Vara Blanca, north slope of Cordillera Central, between Poas and Barba volcanoes: *Skutch 4684,* (US, CM, NY, MBG, WEM), *4686* (US, CM, WEM); La Palma de San Ramón: *Brenes 6300* (CM). GUATEMALA: Dept. Huehuetenango: Cerro Negro: *Steyermark 51690* (CM); between Xoxlac and Nucapuxlac: *Steyermark 48955* (CM). Dept. Suchitepequez: Volcan Santa Clara: *Steyermark 46832* (CM). Dept. Quezaltenango: between Finca Pirineos and Patzulin: *Standley 86951, 86967, 86978, 86981, 86985, 87010* (all CM). PANAMA: Chiriqui-Boquete region: *Von Hagen and Von Hagen 2096* (MBG), *2179* (MBG) (these specimens, collected in 1940, are the first records for Panama of any member of the Juglandaceae).

Flowers appear in early February with possibly others in May, fruit from March to April with possibly another group from July to August.

Standley (1927a) and Skutch have pointed out that *A. costaricensis* is extremely variable, the hairiness of twigs, leaf rachises, and leaflets varying from brown-hirsute to glabrous, the apices of the leaflets from strongly acuminate to acute or even obtuse, and the margins of the leaflets from strongly serrate or dentate to entire. In general the first-mentioned features of each group are characteristic of young growth, or stump sprouts, the second of mature growth. Various combinations and intermediates are to be found between. Thus *Dita Keith 371, Skutch 4686* (at Chicago Museum), *Standley 39217, Standley & Torres 50874* represent characteristic sterile specimens of young growth. *Brenes 6300, Skutch 4686* (the writer's personal herbarium) have hairy twigs and rachises, but the serrate leaflets are entirely glabrous. Characteristic mature flowering specimens, the flowers mostly pistillate, are *Skutch 4684, Standley 33620,* and *Lankaster 1922. Standley & Torres 50870, Standley & Torres 50986,* and *Lankaster 1929* are fruiting, only the last having mature fruit. The other specimens listed represent sterile material in various conditions. It should be stated that identifica-

tion of sterile material is uncertain; some specimens may represent a different species, or might even belong in the genus *Engelhardtia*. The Guatemalan collections especially appear somewhat different.

In all of the specimens listed above either the twigs, rachises, or leaflets are hairy or often all three, and the buds are densely brown-hirsute. *Skutch 4685*, a tree with staminate catkins only, is similar to the above specimens in general leaf type and arrangement, but differs sufficiently in certain respects to warrant describing it as a new variety.

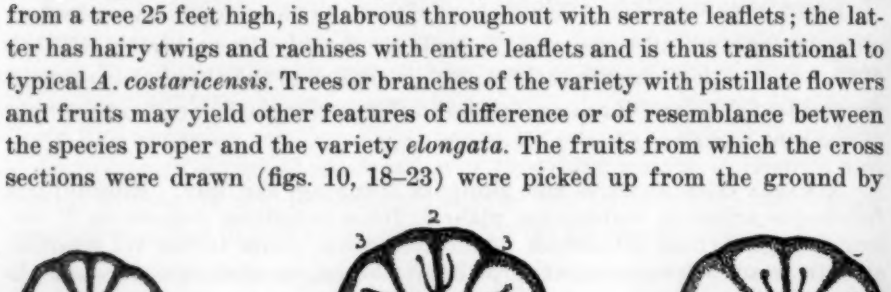
ALFAROA COSTARICENSIS var. **elongata** Manning, var. nov. Rhachidibus foliolisque arborum maturorum glabris; foliis petiolatis, petiolo ca. 2 cm. longo; jugis primis foliolorum paullo minoribus quam tertiis vel quartis; amentis staminiferis elongatis, pedulis; florum masculorum receptaculo elongato.

Twigs, rachises, and leaflets absolutely free of hairs; leaves short-petioled; the first leaflets, not so greatly reduced as in typical *A. costaricensis*, with their points of attachments usually 2 cm. (1.5–3.0 cm.) from the stem; leaflets on both sterile and flowering shoots rather narrowly oblong, acute or abruptly acuminate at the apex, obliquely tapering at the base; most of the buds glabrous (only one bud from several specimens having been found with a few brown hairs at its tip); trees apparently dioecious, the slender, greenish, flexible staminate catkins occurring in ample panicles (4–8 catkins each 4–9 cm. long), the panicles terminal on the principal leafy shoots and on short often essentially leafless side shoots located at the tip of the old growth; most of the individual flowers essentially sessile, with receptacles of an elongate type (ellipsoidal to lenticular). TYPE at US: *Skutch 4685*, Vara Blanca, Costa Rica, north slope of Cordillera Central between Poas and Barba volcanoes, February 15, 1940; isotypes at NY, CM, MBG, WEM.

In typical mature *A. costaricensis*, on the other hand, the leaves are essentially sessile, the lowest leaflets much reduced, and usually 1 cm. (0.5–1.5 cm.) from the stem; the leaflets are often oval, obtuse or acute on flowering twigs, abruptly acuminate on sterile shoots, sessile, truncate, or rounded at base; the trees are monoecious, the staminate spikes usually short at the base of the pistillate spikes, only in exceptional cases in separate clusters of about 4–8 long, commonly almost sessile, stoutish, rather stiff brown catkins; the individual flowers, when fully developed as in the long catkins (*Skutch 4684*), are clearly stalked with nearly round receptacles.

The most important features of the variety are the glabrous twigs, rachises, leaflets, buds, the petioled leaves, and the sessile flowers with rather elongate receptacles; the epithet *elongata* refers to the elongate staminate catkins, though it applies equally to other features (petiole, stalk of catkins, receptacle). The specimens drawn were picked to show certain floral features, and do not of course show all characters equally well. Another specimen of *Skutch 4685* had six leaves on the principal shoot, the lower three large and alternate, two of the upper three large, these two and a small one each apparently subtending the lower catkins of the panicle as in *Platycarya*,

Rhus, etc. *Standley & Torres 50969* (El Muñeco, US, AA) and *Standley 39446* (La Estrella, US) are sterile representatives of the variety, both with elongate petioles and comparatively long lower leaflets. The former, from a tree 25 feet high, is glabrous throughout with serrate leaflets; the latter has hairy twigs and rachises with entire leaflets and is thus transitional to typical *A. costaricensis*. Trees or branches of the variety with pistillate flowers and fruits may yield other features of difference or of resemblance between the species proper and the variety *elongata*. The fruits from which the cross sections were drawn (figs. 10, 18–23) were picked up from the ground by



FIGS. 18–23. *Alfaroa costaricensis* Standley (exact variety uncertain, but probably not var. *elongata*); cross sections of fruit, arranged from base (fig. 18) to apex (fig. 23), showing primary, secondary, and tertiary septa (1, 2, 3 respectively), with lamellae (plate-like outgrowths from septa) at certain levels.

Skutch, and the nature of the leaves of the tree from which it came is unknown. *Lankaster 1929* has similar fruit.

The differences given above are at the same time striking and intangible. It is both remarkable and significant that the differences between *A. costaricensis* and its variety *elongata* are nearly identical with the differences between *Engelhardtia spicata* and its varieties *aceriflora* and *Colebrookiana* [for many years these were considered distinct species, until Koorders and Valeton (1900) pointed out that all differences fluctuated]. *E. chrysolepis* also varies from monoecious to possibly dioecious and is quite diverse in leaves and fruit.

Standley (1927a) described the genus as closely related to *Juglans*. He stated that *Alfaroa* differed in having opposite leaves, no terminal leaflet, smooth instead of rugose nuts, very short instead of long, drooping staminate catkins. But there are other more fundamental differences which set these two genera apart within the family. *Alfaroa* has staminate catkins in clusters, these typically in terminal inflorescences, often in the same inflorescence with the pistillate spike, the latter many-flowered; the stigmas are short with the stigmatic tissue on the outside covering the tips; the bract is three-lobed in staminate and pistillate flowers, is practically separate from the ovary, and does not form a husk; bracteoles are much reduced or apparently absent in the pistillate flower; in the fruit tertiary septa are present; the pith is solid, not chambered, and the wood has many scalariform perforations in the vessels, not simple ones, with rays of type heterogeneous I, not heterogeneous II B.

Alfaroa is more closely related to *Engelhardtia*. This relationship has been indicated in studies on the inflorescences, pistillate and staminate flowers (Manning 1938a, b, 1940, 1948) and on the wood anatomy (Kribs 1927, Heimsch & Wetmore 1939). The flower and fruit features in common between these two genera, many of them indicated in the paragraph above as differences between *Juglans* and *Alfaroa*, are indicated in table 1.

The genus is especially close to the American species of *Engelhardtia*: *E. pterocarpa* (Oersted) Standley (*E. Oreamunoa* DC.), *E. mexicana* Standley, and *E. guatemalensis* Standley. The first species, which was considered by Oersted (1856, 1870) to constitute a genus *Oreamunoa* distinct from the Asiatic species of *Engelhardtia*, was placed by de Candolle (1862, 1864, 1914) in a special section *Oreamunoa* of the genus *Engelhardtia*. Oersted (1870), in his second discussion of the generic characters of *Oreamunoa*, stressed the shape of the stigmas (though he incorrectly described the stigmas of *E. spicata* as always four—see Manning 1940), the four-celled instead of a two-celled condition in the ovary (should be eight-celled instead of two-four-celled), the similarity in the form of the seed to that of the embryo (cotyledons), and the fact that the cotyledons are not entangled but separate from each other though bent and folded. Engler (1889) copied some of the errors of Oersted in his key to the genera. In many ways *Alfaroa costaricensis* seems so close to the American species of *Engelhardtia* that it might be placed as a species in this genus *Oreamunoa;* the internal structure of the fruit, as indicated earlier, is almost identical; other features in common are shown in the table.

The decision on whether to recognize *Oreamunoa* or *Alfaroa* depends upon which criteria, of the many similarities and differences that can be given, one should emphasize. Studies of the inflorescences and flowers have shown that many distinguishing characters vary tremendously within a

TABLE 1. *Comparison of Alfaroa with certain genera and species.*

	Alfaroa	*Engelhardtia pterocarpa*	*Engelhardtia mexicana*	*Engelhardtia chrysolepis*	*Engelhardtia spicata*	*Juglans*	*Pterocarya*
Leaves	(alternate) opposite or whorled	(alternate) opposite	opposite	alternate	alternate	alternate	alternate
Leaflets	thin	thick	thick	thick	thin	thin	thin
Terminal leaflets	absent	absent	absent	absent	absent	present (or absent)	present
Pith	solid	solid	solid	solid	solid	chambered	chambered
Staminate & pistillate inflorescence combined?	androgynous (or separate)	androgynous	(androgynous ?)	androgynous or separate	androgynous or separate	separate	separate
Inflorescence containing staminate catkins	terminal	lateral	lateral ?	terminal	lateral	lateral	lateral
Pistillate inflorescence	terminal	lateral	lateral	terminal	lateral	terminal	terminal
Staminate catkins	clusters	clusters	?	clusters	clusters	solitary	solitary or clusters
Staminate catkins	short or long	long	?	long	long	long	long
Staminate bract	3-lobed	3-lobed	3-lobed	3-lobed	3-lobed	entire	entire
Staminate flowers	stalked or sessile	sessile	?	stalked	sessile	stalked or sessile	stalked or sessile
Staminate floral receptacle	round or elongate	elongate	?	round	elongate	round or elongate	round or elongate
Stamens	6–10	16–23	?	12	2–6	7–105	5–31
Anthers	glabrous	glabrous	?	glabrous	pubescent	glabrous	glabrous
Pistillate flowers	many	many	many	many	many	few to several	several to many
Pistillate flowers	sessile	short-stalked	short-stalked	stalked	sessile or short-stalked	sessile	sessile
Pistillate bract	3-lobed	3-lobed	3-lobed	3-lobed	3-lobed	entire	entire
Pistillate bract	broad	broad	broad	broad	broad	narrow	narrow
Pistillate floral sepals	present	present	present	present	present	present	present
Pistillate bract and ovary	separate	partly separate	partly separate	partly separate	partly separate	fused	separate
Pistillate bracteoles and ovary	separate	partly separate	partly separate	partly separate	partly separate	fused	mostly fused
Pistillate bracteoles	small	small	small	small	small	broad	broad
Carpels	median	median	median	median	median	median	median

TABLE 1. *Comparison of Alfaroa with certain genera and species.—(Cont'd.)*

	Alfaroa	*Engelhardtia pterocarpa*	*Engelhardtia mexicana*	*Engelhardtia chrysolepis*	*Engelhardtia spicata*	*Juglans*	*Pterocarya*
Stigmas	carinal	carinal	carinal	split-carinal	commissural	carinal	carinal
Stigmatic area	short round	short round	short round	short hidden	long	long	long
Fruiting bract	scale	3 wings	3 wings	3 wings	3 wings	fleshy husk (narrow)	scale
Fruiting bracteoles	scale	small wing	small wing	small wing	small wing	large fleshy husk	2 large wings
True husk	absent	absent	absent	absent	absent	present	absent
Tertiary septa	present	present	present	absent	absent	absent	absent
Cotyledons (in fruit)	separate	separate	?	entangled	entangled	separate	entangled
Cotyledon (at germination)	?	?	?	epigaeous	epigaeous	hypogaeous	epigaeous
Fruit (ovary)	hairy	glabrous	glabrous	glabrous	hairy	hairy	glabrous
Nut	smooth	smooth	smooth	smooth	smooth	ridged	ridged
Fruit (nut)	large	medium	small	very small	very small	large	small

genus, especially *Engelhardtia,* and it is difficult to choose true generic criteria. It is clear that the only reliable features are the position in flower and the condition in fruit of the bract and bracteoles (prophylls), associated with similar calyx, carpel, and inflorescence characters.

On these bases *Oreamunoa* is not a good genus, and *Alfaroa* should be recognized. The species of the genus *Oreamunoa* proposed by Oersted and the Asiatic species of *Engelhardtia* are held together in the latter genus by having, as shown in table 1, identical sepal, carpel, and inflorescence features, and a three-lobed bract united with only the lower half of the ovary and much enlarged in fruit for wind dissemination; the body of the fruit (the nut) is relatively small, too (up to 1 cm. long), that of *E. mexicana* forming the connecting link between the very small Asiatic and the larger American forms; *E. mexicana* is also intermediate in its stigma size between *E. chrysolepis* and *E. pterocarpa* (see figures in Manning 1940).

Alfaroa differs from all other genera in the *Juglandaceae* in having neither bract nor bracteoles specialized in fruit; thus its fruiting bract is very small, a scale at the base of the nut, and the bracteoles even more reduced, so that the fruit has neither true husk nor wings; its relatively large nut (over 2 cm. long) is associated with a type of dissemination other than the wind. Occasional abnormal (?) regular-sized fruits of *Engelhardtia chrysolepis* with the fruiting bract remaining small (this form called *E. fenzelii* by Merrill) show how the small bract of *Alfaroa* might have arisen. The apparent absence or great reduction of bracteoles in the pistillate flowers and fruit is associated with the closely sessile flower. The genus *Alfaroa* differs also from other genera in having in some inflorescences one–few-flowered staminate spikes, but these merely represent stages in the complete separation of pistillate and staminate catkins, a condition present in many members of the family. Other features of leaflets, inflorescences, pistillate flowers, fruits and stamens, separating *Alfaroa* from *Engelhardtia pterocarpa* and *E. mexicana,* constituting the proposed genus *Oreamunoa* of Oersted, are indicated in the table. *Alfaroa,* though a weak genus closely related to *Engelhardtia* sect. *Oreamunoa,* is as distinct from *Engelhardtia* as *Juglans* is from *Pterocarya,* where the real critical differences are in the position in flower and the condition in fruit of the bract and bracteoles.

Alfaroa is a very primitive member of the *Juglandaceae;* its primitive features are in its stigmas, calyx, fruit structure, inflorescence type and position, and wood anatomy; its staminate flowers are somewhat advanced. *Alfaroa* and *Engelhardtia pterocarpa* have sprung from a common ancestor.

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Note: Since the above was sent to press, an excellent article on the Juglandaceae and other families by Dr. Hakon Hjelmqvist has appeared ["Studies on the floral

morphology and phylogeny of the Amentiferae'' (Bot. Not. Suppl. 2[1]: 1–171. 1948)]. Dr. Hjelmqvist adopts a different interpretation for the floral parts of various members of the Juglandaceae, including *Alfaroa*, considering the three-lobed bract in both staminate and pistillate flowers of this genus as a bract and two bracteoles; he illustrates the cross-section of the fruit of *Alfaroa* as only 4-celled, and erroneously interprets the stigmas as commissural; the genus *Oreomunnea* (*Oreamunoa*) is recognized, and the inflorescence of *O. pterocarpa* (*Engelhardtia pterocarpa*) is shown to be terminal on the main shoots, not lateral.

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BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 76, NO. 3, PP. 210–212 MAY 1949

A NEW SPECIES OF CARLUDOVICA (CYCLANTHACEAE) FROM SOUTHERN MEXICO

EIZI MATUDA

Carludovica chiapensis Matuda, sp. nov. Planta epiphytica scandens cum radicibus adventitiis, caudice crasso dense 3–5 cm. diam.; folia magna longipetiolata, coriacea et fibrosa; petiolo 65–75 cm. longo ca. ½ longitudine vaginato, lamina basi acute attenuata 70 cm. longa medio ca. 30–35 cm. lata apicem versus ca. ½ longitudine bifida a segmentis 15–17 latis apicem acutis, 14-vel 16-nervatis; pedunculis 15–20 cm. longis crassis, in vivo striatis; spatharum nodis 6, albidis, concavis, 10–15 cm. longis, deciduis; spadice simplici, in vivo cylindrico 6–8 cm. longo, 1.5–2 cm. diam. apice rotundato; floribus femineis parvis concrescentibus ca. 1.5 mm. diam.; perianthio saepe 4-lobato, lobis rotundatis, stigmatibus sessilibus parvis ca. 1 mm. diam. in apicem ovarii confluentibus cruciformibus; floribus masculis parvis ca. 3 mm. diam. perianthio inaequali 6 lobato, lobis acutis; staminibus numerosis, filamentis brevibus, antheris oblongis bilocularibus; staminodiis luteis filiformibus, deciduis, 15–20 cm. longis, in floribus femineis 4 perianthio et stigmate interjectis.

MEXICO: Chiapas: Finca Corcega, about 14 km. northeast of Pueblo Nuevo Comaltitlan (a Pan-American Railway Station), on wet mixed forest, at 900 m. altitude, April 19, 1948, *Matuda 17694;* TYPE in Matuda Herbarium, isotypes in the Instituto de Biología of Mexico, Museo de Dirección General de Agricultura of Mexico, and the Chicago Natural History Museum. Local name: "Tepejilote."

C. latifrons Drude, apparently is closely related, but the larger leaves and 6 spathes amply distinguish *C. chiapensis* from that Brazilian species. Another affinity is with *C. utilis* of Costa Rica, but from this our species with its deciduous spathes and larger leaf can be separated readily. As far as I am aware, this is the first record of the genus from Chiapas. The only other Mexican record we have is *C. gracilis* from Oaxaca. All descriptions hitherto published in the genus are deficient in their characterization of the very small floral organs. Fortunately I have secured sufficient fresh material of the present species and it was possible to observe all the characters of these floral structures. The surface of the spadix is covered with numerous long staminodes and the staminate flowers contain numerous oblong anthers as shown in figure 2. Figure 3 shows pistillate flowers after the staminodes and staminate flowers were carefully removed, leaving only their vestiges. The male flowers are practically located two by two vertically. The 6-lobed perianth is developed only at the outside of the pair of flowers as shown in figure 7; the inner side is entirely destitute of perianth. It is possible to say that one female flower is surrounded by eight

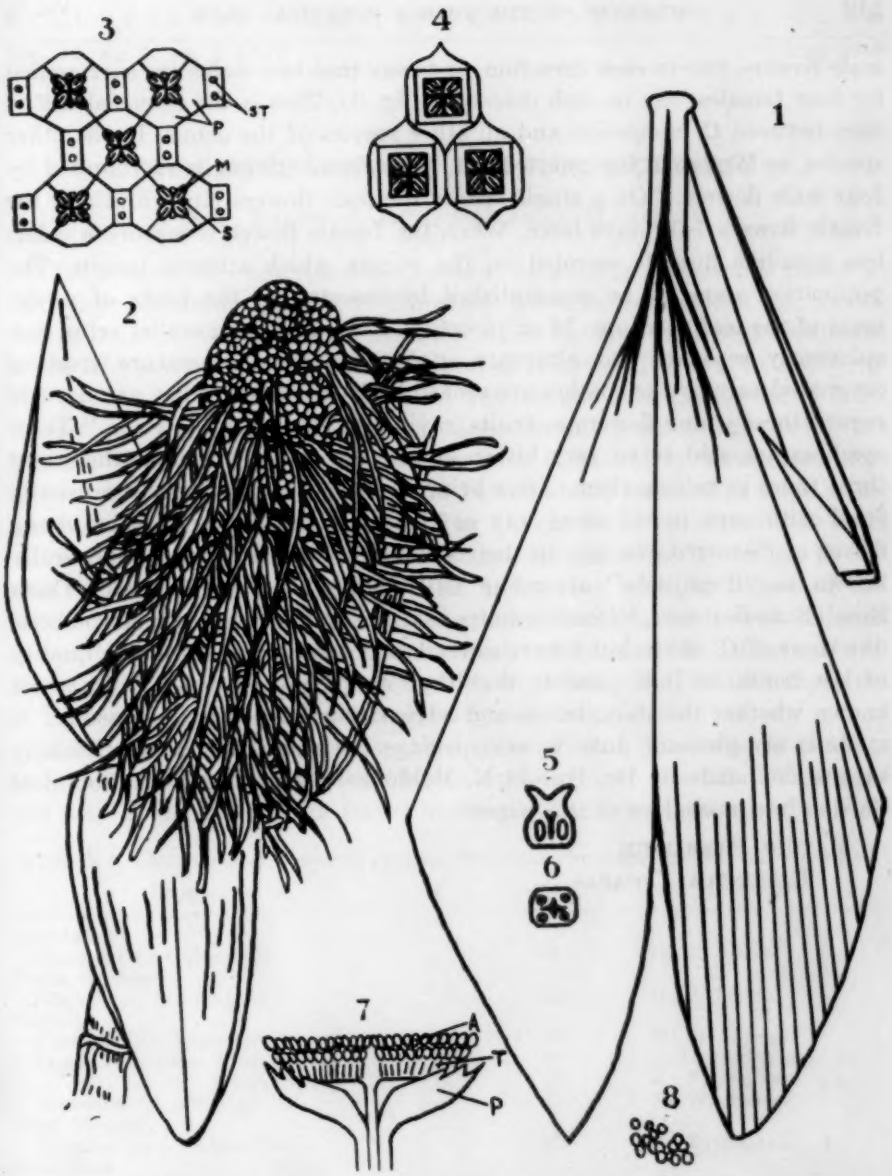

FIG. 1. General aspect of leaf. × ⅙. FIG. 2. General aspect of mature flower opened. × 1. In the upper part of the spadix the staminodes are already fallen, exposing the concourse of anthers. Upper three spathes shown. Staminodes cut lengthwise. FIG. 3. Female flowers covering the spadix, exposed by removal of male flowers and staminodes. × 5. M, cruciform stigma. P, perianth. S, vestige of staminodes, four in each female flower. St, vestige of male flower, showing two vertical colocations. FIG. 4. Surface of spadix when fruits are ripe. Stigma and perianth also developed, greenish-yellow. Stigma and perianth fallen, exposing juicy yellow naked fruits which contain 4–12 small, thin, oblong seeds. Length of seed approximately 0.5 mm. FIG. 5. Female flower, vertical section. × 4. FIG. 6. The same, horizontal section of ovary. × 4. FIG. 7. Pair of male flowers. × 6. P, perianth. A, anthers. F, filaments. FIG. 8. Pollen. × 80.

male flowers, two in each direction, or to say that two males are surrounded by four females, one in each direction (fig. 3). This is the essential difference between *C. chiapensis* and all other species of the genus. In the other species, as Wettstein has pointed out, "one female flower is surrounded by four male flowers." On a single spadix the male flowers ripen first and the female flowers 7–10 days later. When the female flower is mature a colorless gum-like fluid is secreted on the stigma which attracts insects. The pollination seems to be accomplished by insects. On the blade of a segment of the leaf there are 14 or 16 semipalmate and semiparallel veins conspicuously separate and alternate on both surfaces. Immature spadices covered closely by the spathes are cooked by local natives. They erroneously regard these young flowers as fruits, saying "Fruta tierna se come." These spadices are said to be very bitter so that one needs to renew the water three times in boiling them. After being thoroughly boiled they are usually fried with eggs in the same way as the so-called "Pacaya" (the young flower of *Chamaedorea* spp. in their sheaths) which in Oaxaca is generally known as "Tepejilote" according to Standley. In his "Flora of Costa Rica" Standley says, "Oersted states that the Indians ate the ripe spadices, like those of *C. utilis*, but I have never heard mention of the edible quality of the fruits, so it is possible that they are no longer eaten." It is not known whether the stalk, leaves and adventitious roots are used locally.

It is my pleasant duty to acknowledge the many favors and friendly suggestions made by Dr. Harold N. Moldenke of the New York Botanical Garden in preparation of this paper.

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BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 76, NO. 3, PP. 213–216 MAY 1949

CYTOGEOGRAPHY OF SAURURUS CERNUUS

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The geographic occurrence of *Saururus cernuus* L. is shown in figure 1: from near Montreal, Quebec, to Wingham, Ontario, to Gonzales Co., Texas, and to Dade Co., Florida. The small circles on the map represent specimens in the Herbarium of the Chicago Natural History Museum, in the Gray Herbarium, or in the U. S. National Herbarium, and give records from Palmer and Steyermark (1935) for Missouri and from Deam (1940) for Indiana. To forestall erroneous impressions it should be recognized that concentrated records for Missouri and Indiana have resulted in large measure from definite floristic programs. The big circles indicate localities from which specimens have been collected for cytological study. There are twelve such localities; they are listed in table 1, together with the names of collectors. The distributional area of the species has been fairly well sampled except for the southwestern portion. Twelve specimens of *Baldwin 12014*, Williamsburg, James City Co., Virginia, August 8, 1948, will be deposited in herbaria as records of plants cytologically examined.

Saururus cernuus, commonly called "lizard's tail," is found in marshes and wet woods and along ditch banks and edges of streams. "Traces of salt may be the influencing factor in the distribution of the plant" (Wie-

TABLE 1. *Collections of Saururus cernuus for which chromosomes have been counted.*

Source	n	$2n$	Collector
Florida			
Alachua Co.: Gainesville		22	O. E. White
North Carolina			
Essex Co.: Wilmington		22	O. E. White
Virginia			
Norfolk Co.: Lake Drummond		22	B. M. Speese
James City Co.: Williamsburg		22	J. C. Strickland, Jr.
: Williamsburg	11	22	J. T. Baldwin, Jr.
Lancaster Co.: Weems		22	R. W. Menzel
West Virginia			
Berkeley Co.: Hedgesville		22	J. T. Baldwin, Jr.
New York			
Genesee Co.: Black Creek		22	B. L. Brown
Indiana			
Wells Co.: Salamonie River		22	C. C. Deam
Illinois			
Champaign Co.: Urbana		22	S. A. Watson
Missouri			
Franklin Co.: Pacific		22	R. E. Woodson, Jr.
Kentucky			
Trigg Co.: Rockcastle		22	A. M. Harvill
Alabama			
Tuscaloosa Co.: Tuscaloosa		22	A. V. Beatty

gand & Eames 1926). The species "shows a wide acidity tolerance and is found in acid and alkaline regions alike. It is very often found in association with *Anopheles quadrimaculatus* and in some instances constitutes a major problem" (Eyles & Robertson 1944). It has become a pest in some of the reservoirs constructed by the Tennessee Valley Authority (Hall 1940). Its

FIG. 1. Distribution of *Saururus cernuus*. Small circles indicate herbarium and literature records; big circles show origin of plants cytologically examined.

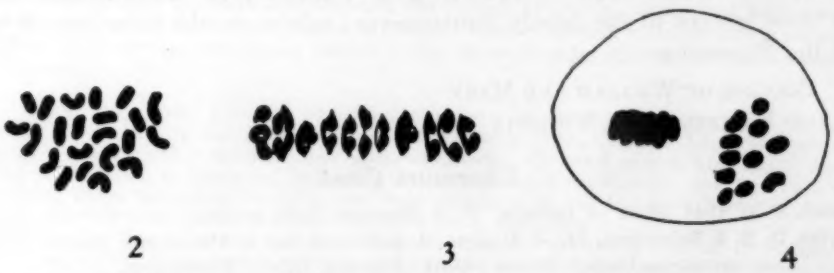
populations vary in size from a few individuals to millions. It readily propagates itself both by vegetative means and by seed. Hall (1940) estimated that about twenty thousand seed per square foot of colony of *Saururus* are produced each year.

This plant has a $2n$-number of 22, n-number of 11 (figs. 2–4). Propio-

carmine smears of very young leaves evidenced many mitoses and were good for study. Smears of pollen mother-cells were especially clear, and all meiotic stages were found in the anthers of a single flower. This material would be excellent for class use. From hematoxylin preparations of microsporogenesis Täckholm and Söderberg (1918) determined the *n*-number of this species to be 10.

Saururus chinensis (Lour.) Baill. is the only other representative of the genus. We have seen herbarium specimens from Japan, Formosa, southeastern China, French Indo-China, and the Philippines. Seemingly the chromosomes have not been investigated.

Houttuynia Thunb., with one species in Japan, China, and the Himalaya region (Söderberg 1927), and *Anemopsis* Hook., with one species from New Mexico to southern Utah, Nevada, and southern California to Mexico (Tidestrom & Kittell 1941), are closely related to *Saururus*. These three genera and four species are referred by some authors to the family Saururaceae



FIGS. 2–4. Chromosomes of *Saururus cernuus*. FIG. 2. Mitotic metaphase from leaf. FIG. 3. Metaphase I of microsporogenesis. FIG. 4. Metaphase II of microsporogenesis. Magnification × 2200.

and by others to the tribe Saurureae of the Piperaceae. In having three or four free or united carpels with two or more non-basal ovules these genera stand apart from the Piperaceae proper, which have a one-celled ovary with a single basal ovule (Rendle 1938). And there are likewise marked differences in vascular tissue (Solereder 1908).

Shibata and Miyake (1908) reported *Houttuynia cordata* Thunb. to be parthenogenetic, with abortive pollen and with a $2n$-number of 52–56. Söderberg (1927) questioned the existence of apogamy in this plant and recorded that $2n$ = 100–104, n = ca. 50. Okabe (1930) arrived at a $2n$-number of 94–98 and discovered meiosis to be irregular at both micro- and megasporogenesis, but in some cases the megaspore mother-cell exhibited only univalents with resultant diploid embryo-sacs which developed parthenogenetically. According to one of Tischler's chromosome lists Okabe in 1934 reported the $2n$-number of this species to be ca. 96.

The chromosomes of *Anemopsis californica* (Nutt.) Hook. and Arn. have not been examined.

As living plants for the other three species of this complex come to hand, we plan to investigate them for chromosomal comparison with *Saururus cernuus*.

SUMMARY

Saururus cernuus has a geographic range from Montreal, Quebec, to Texas and to Florida. It often forms extensive colonies affording excellent breeding places for anopheline mosquitoes, and, for that reason, the plant is considered a pest.

Chromosome counts for plants from twelve localities have been made: $2n = 22$, $n = 11$. An n-number of 10 has been reported by other workers.

Saururus likewise has a species in Asia. *Houttuynia* is a related monotypic genus in Asia; for it differing chromosome numbers and conflicting accounts of parthenogenesis are in the literature. *Anemopsis* is a second monotypic genus showing affinity to *Saururus;* it is in the southwestern United States and adjacent Mexico. Some authors refer these four species in three genera to the family Saururaceae; others, to the tribe Saurureae of the Piperaceae.

COLLEGE OF WILLIAM AND MARY
WILLIAMSBURG, VIRGINIA

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BULLETIN OF THE TORREY BOTANICAL CLUB

VOL. 76, NO. 3, PP. 217–222 MAY 1949

TORREYA

Arthur Dobbs (1750) and the Discovery of the Pollination of Flowers by Insects. It is stated in all historical accounts of the subject that Joseph Gottlieb Kölreuter was the first to point out that insect visits are necessary for the pollination of flowers.[1] Kölreuter himself apparently regarded his discovery as unprecedented, for he exclaims that: "Gewiss, ein ieder anderer, der vor mir diese Betrachtungen angestellt hätte, würde sie längst entdeckt, und sich und allen Naturforschern von diesem Geheimnisse der Natur den Vorhang weggezogen haben.[2] As it happens "ein ieder anderer" had indeed already discovered that flowers are pollinated by bees and had communicated this observation to the Royal Society of London in 1750. It cannot diminish the fame of Kölreuter, whose greatness really consisted in his experimental approach to sexuality and hybridization in plants, to record at this belated date the contributions of a certain Arthur Dobbs in Ireland.

Having perused the entomological memoirs of M. de Réaumur[3], Mr. Dobbs finds that he differs from that authority on two particulars. Réaumur has stated that wax is formed internally in bees and is discharged through the mouth, whereas Dobbs has observed it to be excreted through the anus. Furthermore, the French naturalist claims that bees roam from the flowers of one species of plant to those of another species while gathering pollen, and this Dobbs denies. Addressing himself to the Royal Society, Arthur Dobbs discourses as follows:

"As to the [latter point in which I differ from M. *Reaumur*], I have frequently follow'd a Bee loading the *Farina*, Bee-Bread, or crude Wax, upon its Legs, through a Part of a great Field in Flower; and upon whatsoever Flower I saw it first alight and gather the *Farina*, it continued gathering from that Kind of Flower; and has pass'd over many other Species of Flowers, tho' very numerous in the Field, without alighting upon or loading from them; tho' the Flower it chose was much scarcer in the Field than the others: So that if it began to load from a Daisy, it continued loading from them, neglecting Clover, Honeysuckles, Violets, &c.; and if it began with any of the others, it continued loading from the same Kind, passing over the Daisy. So in a Garden upon my Wall-Trees, I have seen it load from a Peach, and pass over Apricots, Plums, Cherries, &c. yet made no Distinction betwixt a Peach and an Almond.

"Now M. *Reaumur*, in his Memoir upon the Bee's making Honey, mentions *Aristotle's* Observation of the Bee's loading or gathering from one Species of Flower without changing; not quitting a Violet to gather from a Cowslip; which he says is not justly founded; for he has observed frequently a Bee on a large Border gathering from Flowers of different Species. If M. *Reaumur* only means, that, when the Bee gathers Honey, it takes it indifferently from any Flower, I can say nothing against it; but, if he intends it to mean the Bee's loading the *Farina* upon its Legs, then my Observation directly contradicts it.

"What further confirms my Observation is this, that each Load upon the Legs of a Bee is of one uniform Colour throughout, as a light Red, an Orange, a Yellow, a White, or a Green, and is not upon different Parts of the Load of a different Colour; so that as the *Farina* of each Species of Flowers, when collected together, is of one uniform Colour, the Presumption is, that it is gather'd from one Species. For, if from different Kinds, Part of the Load might be of one Colour, and Part of another.

"Another Observation to confirm the same Fact is, that Bees, in the Height of the Season, return to their Hives with Loads of very different Magnitudes, some having Loads as great as small Shot, whilst others have very small Loads; it cannot be conceiv'd that

[1] **Müller, H.** The fertilization of flowers. 1883. [transl. D'Arcy Thompson, London.] **Sachs, J.** History of botany (1530–1860). 1890. [transl. H. E. F. Garnsey, Oxford.] **Knuth, P.** Handbook of flower pollination. 1906. [Transl. A. Davis, Oxford.] **Nordenskiöld, E.** The history of biology. New York and London, 1928. **Reed, H. S.** A short history of the plant sciences. Waltham, Mass., 1942.

[2] **Kölreuter, J. G.** Vorläufige Nachricht von einigen das Geschlecht der Pflanzen betreffenden Versuchen und Beobachtungen. Leipzig, 1761–1766.

[3] **Réaumur, M. de.** Mémoire pour servir à l'histoire des insectes. Paris, 1740. [vol. 5.]

this Difference is from the Inactivity or Sloth of the Bee in collecting its Load, but rather from the Scarcity of the Flowers, upon which it first began to Load.

"Now, if the Facts are so, and my Observations true, I think that Providence has appointed the Bee to be very instrumental in promoting the Increase of Vegetables; but otherwise, might be very detrimental to their Propagation; and at the same time they contribute to the Health and Life of their own Species.

"From the late Improvement made by Glasses, and Experiments made, in observing the Works of Nature, it is almost demonstrable, that the *Farina* upon the *Apices* of Flowers is the Male Seed; which entering the *Pistillum* or *Matrix* in the Flower, impregnates the *Ovum*, and makes it prolific. . . Now, if the *Farina* of specifically different Flowers should take the Place of its own proper *Farina* in the *Pistillum*, like an unnatural Coition in the animal World, either no Generation would happen, or a monstrous one, or an Individual not capable of further Generation.

"Now if the Bee is appointed by Providence to go only, at each Loading, to Flowers of the same Species, as the abundant *Farina* often covers the whole Bee, as well as what it loads upon its Legs, it carries the *Farina* from Flower to Flower, and by its walking upon the *Pistillum* and Agitation of its Wings, it contributes greatly to the *Farina's* entering into the *Pistillum*, and at the same time prevents the heterogeneous Mixture of the *Farina* of different Flowers with it; which, if it stray'd from Flower to Flower at random, it would carry to Flowers of a different Species."[4]

We may set the foregoing statements of Dobbs against the historical background. In 1694 Rudolf Jacob Camerarius[5] had demonstrated experimentally the existence of sexual reproduction in plants. The question which next arose was how, in the natural course of events, the pollen is conveyed from the anthers to the stigmas. That question was answered some years later in Germany by Kölreuter, who explained that some flowers are pollinated by insects and others by wind. Christian Konrad Sprengel subsequently revealed that the true role of insects was to convey pollen from one flower to the stigmas of another flower, since: "die Natur [scheint] es nicht haben zu wollen, dass irgend eine Blume durch ihren eigenen Staub befruchtet werden soll."[6] The biological significance of this emphasis on cross-pollination in the plant kingdom was first perceived by William Herbert, who noted that the progeny of artificial outcrosses of *Hippeastrum* were more vigorous than seedlings derived from self-fertilizations.[7] Darwin, taking the matter up at this point, announced the generalization (really an erroneous overgeneralization as it later turned out) that nature "abhors perpetual self-fertilisation."[8] Such in outline is the development, by the first experimental geneticists, of the doctrine of sexuality in plants.

The observations and deductions of the Irish amateur, when viewed in the time scale, outrange those of the earliest geneticists at both ends. To begin with, he has repeated and confirmed the ancient observation of Aristotle[9] to the effect that bees remain constant to one kind of flower at a time; and he has correctly noted that the flower constancy of bees is more rigorous when they are gathering pollen than when they are taking nectar. These facts were not revived again, so far as I have been able to learn, until the time of Darwin.[10] The lines of evidence which Dobbs adduces in support of the thesis of flower con-

[4] See the list of Dobbs' titles at the end of this paper. The quotation is from p. 538–540 of the last paper.

[5] **Camerarius, R. J.** De sexu plantarum epistola. 1694. [transl. M. Möbius in Ostwald's Klassiker, Leipzig, 1899.]

[6] **Sprengel, C. K.** Das entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen. Berlin, 1793. [p. 56.]

[7] **Gärtner, C. F.** Versuche und Beobachtungen über die Befruchtungsorgane der vollkommeneren Gewächse und über die natürliche und künstliche Befruchtung durch den eigenen Pollen. Stuttgart, 1844. **Knight, T. A.** An account of some experiments on the fecundation of vegetables. Philos. Trans. Roy. Soc. **89**: 195–204. 1799. **Herbert, W.** Amaryllidaceae; preceded by an attempt to arrange the monocotyledonous orders and followed by a treatise on crossbred vegetables, and supplement. London, 1837.

[8] **Darwin, C.** The various contrivances by which orchids are fertilised by insects. London, 1862. [ch. 9.]

[9] **Aristoteles.** Historia animalium. [Transl. D'Arcy Thompson, Oxford, 1910; bk. 9, ch. 40, p. 624b.]

[10] **Darwin, C.** The effects of cross and self fertilisation in the vegetable kingdom. London, 1876. [ch. 11.] **Bennett, A. W.** On the fertilisation of certain Labiatae. Nature **10**: 92, 93. 1874.

stancy have a modern ring; the examination of the pollen loads of bees for the purpose of estimating the fidelity of their visits to one kind of flower is a technique which is being used currently (for example, Brittain and Newton in 1933[11]).

With regard to the manner of the pollination of flowers by bees, Dobbs has brought out two conclusions of great importance: first, bees carry the pollen from one plant to another of the same species, and so effect cross-fertilization; secondly, they do not take the pollen from the flowers of one species to those of another, and, to the extent that they do not, they prevent interspecific hybridization. Darwin, who knew of Dobbs' work and cited it, understood very well the first fact, but appears to have missed entirely the significance of the second deduction. "That insects should visit the flowers of the same species as long as they can, is of great importance to the plant, as it favors the cross-fertilisation of distinct individuals of the same species," he wrote in 1876 (ch. 11); but he did not add: and it also prevents the cross-pollination of individuals belonging to different species. The latter deduction pertained to an aspect of pollination studies that was not being emphasized just then. It was not indeed until 1947, when Mather published some experimental results relevant to the species problem in *Antirrhinum*, that anyone seems to have given much thought to the possibility, suggested by Dobbs in 1750, that the flower constancy of bees might operate in nature as an isolating mechanism.[12]

I have gathered little biographical information on Arthur Dobbs, preferring to leave that task for the historian of science. He lived at Castle-Dobbs on the northeast coast of Ireland, near Carrickfergus in the County of Antrim. A list of his contributions to the Royal Society is given at the end of this article. Dobbs was both a careful and a well-informed observer of astronomical phenomena. With regard to the geography of the North Pacific area Dobbs disagrees with Captain Behring that the coast sighted by the latter navigator east of Kamschatka is mainland joined with California, holding it rather to be a great island. His comments on this point are revealing, for they connect him with the search for a Northwest Passage. He speaks as though he has personally "promoted . . . the Attempt . . . [to] sail through" (i.e., from Hudson's Bay to the Pacific Ocean). "A few Months now, if our Ships return safe, will give us a Certainty on one Side or the other . . ." This was in 1747. Three years later (1750) he has his certainty and writes: "Since my View of doing Good, by making Discoveries of the Great World has been disappointed, upon my Retirement into this little Corner of it (*Ireland*) amongst other rural Amusements I have been contemplating the Inhabitants of the Little World; particularly that most useful and industrious Society of Bees."

In conclusion, an Irish country squire and amateur naturalist by the name of Arthur Dobbs published in 1750 some significant observations and deductions concerning the mutual relationships of flowers and bees. Dobbs preceded Kölreuter by a decade in the discovery that bees effect the pollination of flowers, Sprengel by some forty-three years in the conclusion that the activities of the bees cause the flowers to be cross-pollinated; he anticipated Darwin by a century in linking cross-pollination to the flower constant habits of bees, and preceded Mather and the present author by two centuries in pointing out how the flower constancy of bees might operate as an isolating mechanism.—Verne Grant.

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————. 1726. An account of an aurora borealis seen in Ireland in September 1725. Philos. Trans. Roy. Soc. **34**: 128–132.

————. 1729. An observation of the eclipse of the moon at Castle-Dobbs near Carrickfergus in Ireland, Feb. the 2d, 1728–9. Philos. Trans. Roy. Soc. **36**: 140, 141.

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————. 1750. Concerning bees, and their method of gathering wax and honey. Philos. Trans. Roy. Soc. **46**: 536–549.

[11] **Brittain, W. H. & Newton, D. E.** A study of the relative constancy of hive bees and wild bees in pollen gathering. Canad. Jour. Res. **9**: 334–349. 1933.

[12] **Mather, K.** Species crosses in *Antirrhinum*. I. Genetic isolation of the species *majus*, *glutinosum* and *orontium*. Heredity **1**: 175–186. 1947. **Grant, V.** Pollination systems as isolating mechanisms in angiosperms. Evolution **3**: [in press].

Reviews

The Flowers that Bloom in the Spring in Rockland County. By John M. Price. The Rockland Audubon Society, West Nyack, N. Y.

This is a set of six mimeographed sheets making a calendar which lists 144 spring flowers in a table, with the dates of first bloom, the colors, and likely locations. There is a blank column left for the user to list his own first dates. Included are notes on using the calendar, on botanical names, on picking flowers, and on useful flower guides. The work is priced at 15 cents each or $1.00 for ten. It should be a useful model for school projects elsewhere.—T. C. R.

Check-List of the Vascular Plants of Maine. By E. C. Ogden, F. H. Steinmetz and F. Hyland. Bulletin of the Josselyn Botanical Society of Maine, Number 8. August, 1948.

This is a pamphlet of 70 pages reproduced by photooffset from typewritten copy. It lists by families the species of vascular plants found in Maine, with check-marks showing their distribution by counties. The nomenclature is essentially that of *Gray's Manual*, with, however, many corrections due to recent research. The list is based on a painstaking and systematic keeping of records which extends back through many years, and should be of great value for future students of the flora of Maine.

The book may be obtained through Dr. F. H. Steinmetz, Coburn Hall, University of Maine, Orono, for 50 cents prepaid.—H. W. R.

Proceedings of the Club

Minutes of the meeting of January 19, 1949. The meeting was called to order by President Matzke at Hunter College at 8: 10 P.M.; 20 members and friends were present. The minutes of the annual meeting were read and approved.

The president reported that the petition authorized at the last meeting had been prepared and sent. Dr. Laura A. Kolk was elected to serve the unexpired (one-year) portion of Dr. Levine's term as Council Member. The following committees were appointed for the year 1949:

Field Committee: Vernon L. Frazee (Chairman), Louis E. Hand, Harold N. Moldenke, James Murphy, G. G. Nearing, Rutherford Platt, William Rissanen, Farida A. Wiley; *Program Committee:* Jennie L. S. Simpson (Chairman), Charles A. Berger, Harold H. Clum, Marion A. Johnson, Elva Lawton, Edwin B. Matzke, Harold W. Rickett, Donald P. Rogers; *Publications Exchange Committee:* Jennie L. S. Simpson (Chairman), Amy L. Hepburn, Harold W. Rickett.

Dr. James E. Gunckel of Rutgers University spoke on "Growth habit, shoot expression and the mechanism of its control in *Ginkgo biloba.*" His abstract of the address follows:

> Two well-defined types of shoots, namely *long shoots* and *short shoots*, occur in *Ginkgo*. A short shoot of any season may in any season assume the long-shoot habit. Conversely, a long shoot of one or more previous seasons may in any season fail to produce internodal growth and so assume the short-shoot habit.
>
> The excurrent type of growth habit in young Ginkgos is due to the formation of terminal long shoots. The broadening of trees with age is due to changes in shoot expression, the mature trees having equal numbers of long- and short-shoot terminals. The older the plant or the older the buds the less chance for shoot reversal, unless disturbed by an injury.
>
> Decapitation of young plants causes short-shoot laterals to develop into long shoots. Application of napthaleneacetic acid to the cut surface maintains the laterals in the short-shoot condition, as in intact plants, suggesting terminal-bud inhibition for controls.

Approximate rules have been developed for determining in selected cases whether a bud will develop into a long or short shoot. The yield of diffusible auxin from short-shoot buds rises from zero in the "tight" stage to a maximum at first greening and then decreases as the buds open. Long shoots behave similarly, but after the auxin yield has fallen with bud opening it rises steeply with the beginning of elongation. Auxin production by the long shoot in its youngest leaves and internodes then becomes very small, while large amounts are produced by the lower, rapidly extending internodes. The diffusible auxin is in excess of that used in shoot elongation. The total yield per shoot increases with the number of nodes rather than with the length of the shoot. The auxin is not produced by the leaves or the apical meristem, but reasons exist for concluding that it is produced (or activated) in the stem itself, while the young leaves may supply an inactive auxin precursor.

Bud development is considered as taking place in two stages, i.e. (1) opening and leaf enlargement (2) axis elongation and associated growth so that lateral short shoots become a special case of bud inhibition in which only stage (2) is inhibited. However, growth data show that where auxin supply is adequate the ability of long shoots to develop from laterals is also some function of the general nutrition of the plant.

Acropetally developing procambial strands project into the region of presumptive leaf primordia before the primordia appear. This precocious development of the primary vascular system, together with the physiology of shoot growth, are offered as evidence that the pattern of shoot growth is not alone a property inherent in the stem apex, as some have suggested, but that the physiology and pattern of development of older stem tissues are, if not a controlling factor, at least a corollary to shoot growth.

The meeting was adjourned at 9: 40. Refreshments were served by the Hunter staff.

Minutes of the meeting of February 16, 1949. The meeting was called to order at Hunter College by President Matzke at 8: 10 P.M.; 37 members and friends were present. The minutes of the preceding meeting were read and approved; no other business was transacted. Mr. G. G. Nearing of Demarest, N. J., spoke on "Lichens we see on field trips," illustrating his discussion with color photographs.

The meeting was adjourned at 9: 45; afterward refreshments were served by the Hunter College botanists.

Respectfully submitted
DONALD P. ROGERS
Recording Secretary.

Minutes of the meeting of March 1, 1949. The meeting was called to order at Columbia University by President Matzke at 8: 10 P.M.; 22 members and friends were present. The minutes of the preceding meeting were read and approved. Dr. Francis J. Ryan of Columbia University spoke on "Adaptation of biochemical mutants of microörganisms." His abstract follows:

Microorganisms are renowned for their ability to adjust to unfavorable conditions in their environment. For example, a mutant of the mold *Neurospora crassa* which requires the amino acid leucine for growth may adjust to a low concentration of leucine by developing the ability to synthesize this substance. By the use of genetic techniques it has been possible to show that adaptations are the result of back-mutations of genes which cannot enable leucine synthesis to a condition where they can. Such mutations result in a heterogeneous mixture of nuclei within the mycelium and a competition is set up between the two types. The outcome of this competition depends upon environmental conditions which, then, through their selection for or

against mutant genes, will determine whether adaptation occurs. In the bacterium *Escherichia coli* back-mutations in growth-factor-requiring strains similarly return synthetic ability. The competition between back-mutant and parent leads to adaptation when a poor supply of growth factor is present. In the presence of an adequate supply of growth factor an equilibrium is reached so that a growth-factor-requiring culture is stable but always possessed of a few back-mutant growth factor-independent organisms. Thus even the "training" of microorganisms when examined closely turns out to be explained by mutation and selection.

The meeting was adjourned at 9: 45 P.M.

Respectfully submitted
ANNETTE HERVEY
Recording Secretary pro tem.

NOTE

Still another new botanical periodical of international scope has issued its first number. This is *Phyton*, or *Annales Rei Botanicae*, published in Horn, Austria, edited in Graz. The inserted announcement states that the purpose of *Phyton* is to cover the entire field of botany. Articles will be accepted in any of the languages of the International Botanical Congresses. The first issue contains articles on genetics, on taxonomy (including phytogeography), on plant physiology, on pollen analysis, and on several other topics. All but one are in German.

The magazine is well printed on good paper and attractively designed.

INDEX TO AMERICAN BOTANICAL LITERATURE

COMPILED BY

LAZELLA SCHWARTEN

WITH THE COLLABORATION OF THE EDITOR OF THE TAXONOMIC INDEX

TAXONOMY, PHYLOGENY AND FLORISTICS

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FUNGI AND LICHENS

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